

BULLETIN

OF CARNEGIE MUSEUM OF NATURAL HISTORY



SKULL AND ATLAS-AXIS COMPLEX OF THE
UPPER JURASSIC SAUROPOD
CAMARASAURUS COPE (REPTILIA: SAURISCHIA)

JAMES H. MADSEN, JR., JOHN S. McINTOSH, AND DAVID S BERMAN

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Cover illustration: Skull of *Camarasaurus lentus* CM 11338 with left mandibular ramus removed.

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ABSTRACT

The skull, lower jaw, and atlas-axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope are described in detail on the basis of articulated specimens and isolated elements collected primarily from the Cleveland-Lloyd and Dinosaur National Monument quarries in Utah. Two elements heretofore unreported in the sauropod skull and mandible, the stapes and coronoid, are described. Each disarticulated element has been figured in multiple views, and in many instances the same element of several specimens is shown in order to illustrate the range of individual variation. In addition to the

materials from the two principal quarries, all cranial materials known to belong to *Camarasaurus* are listed, and the fragmentary materials belonging to holotypic specimens are also figured. The skull and lower jaw of *Camarasaurus* are compared with those of the prosauropod *Plateosaurus* and other sauropods. Unlike many vertebrate groups the sauropods exhibit greater morphological variation in the postcranial skeleton than in the skull, and therefore any attempt to revise the genus *Camarasaurus* must await the full study of articulated postcranial skeletons.

INTRODUCTION

Since the first discoveries of sauropod dinosaur skeletons in the 1870s, researchers have been frustrated by the almost total absence of skulls. This has been a factor hampering the systematic study of sauropod dinosaurs. With regard to Upper Jurassic sauropods, this situation has been greatly reversed by discoveries at two famous Morrison Formation quarries in Utah, Cleveland-Lloyd and Dinosaur National Monument (formerly the Carnegie quarry of Carnegie Museum of Natural History). Yet, to date, only four Upper Jurassic sauropod genera are represented by complete skulls found associated unquestionably with postcranial skeletons: *Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, and *Diplodocus*. Of these genera the greatest amount of cranial material known today is assignable to *Camarasaurus*, and, although several excellent papers have been published dealing with various aspects of the skull of this genus, no comprehensive description is available. The Cleveland-Lloyd and Dinosaur National Monument quarries have yielded sufficient materials for the present detailed description of the skull of *Camarasaurus* Cope, the first for any American sauropod and the only example for a sauropod other than that of the African *Brachiosaurus* (Janensch, 1935–1936) and the Chinese *Shunosaurus* (Zhang, 1988). The *Camarasaurus* skull materials from the two quarries complement one another well. Those from Dinosaur National Monument are articulated, complete, and well preserved, whereas the Cleveland-Lloyd quarry has yielded only disarticulated elements. This has permitted the study of almost every skull element in multiple views and the description of their precise relationships with adjoining bones.

Throughout the text comparisons are made between *Camarasaurus* and various sauropods and the prosauropod *Plateosaurus*. These are based in

great part on the descriptions of *Antarctosaurus* (Huene, 1929), *Apatosaurus* (Berman and McIntosh, 1978), *Barosaurus* (Janensch, 1935–1936, 1961), *Brachiosaurus* (Janensch, 1935–1936), *Dicraeosaurus* (Janensch, 1936–1936), *Diplodocus* (McIntosh and Berman, 1975; Berman and McIntosh, 1978), *Euhelopus* (Wiman, 1929; Mateer and McIntosh, 1985), *Nemegtosaurus* (Nowinski, 1971), *Plateosaurus* (Huene, 1926, 1932; Galton, 1984), *Pleurocoelus* (Lull, 1911; Kingham, 1962), and *Quaesitosaurus* (Kurzanov and Bannikov, 1983). To avoid unnecessary repetition, these papers will not be continually referred to throughout the text. The only cranial material referable to *Barosaurus* belongs to specimens from the Tendaguru beds of Tanzania and were originally described as *Gigantosaurus africanus* Fraas, 1908. Although the evidence for the subsequent referral of the African species to the North American genus *Barosaurus* by Janensch (1922) is not indisputable, its consideration as a diplodocid is undoubted (McIntosh, 1990b).

The following abbreviations are used to identify repositories of specimens: AMNH, American Museum of Natural History; BYU, Brigham Young University; CM, Carnegie Museum of Natural History; DNM, Dinosaur National Monument; USNM, National Museum of Natural History; UUVP, Cleveland-Lloyd Dinosaur Quarry collections (housed in part at the Utah Museum of Natural History, Salt Lake City, Utah; Earth Sciences Museum, Brigham Young University, Provo, Utah; and College of Eastern Utah, Prehistoric Museum, Price, Utah); YPM, Yale Peabody Museum. The abbreviations r, l, and p, enclosed in parentheses and following a specimen catalogue number, indicate right, left, and paired skeletal elements, respectively.

HISTORICAL REVIEW AND MATERIALS

The first recorded discovery of sauropod skull material, with the exception of isolated teeth, was made by William Harlow Reed, William Edward Carlin, and Samuel W. Williston during the winter

of 1877–78 at Quarry 1, Como Bluff, Wyoming, collecting for O. C. Marsh (Ostrom and McIntosh, 1966). The specimen, YPM 1905, consists of a well-preserved posterior half of skull, incomplete

maxillae, and dentary. It was designated the paratype of *Morosaurus* (= *Camarasaurus*) *grandis* and was described briefly by Marsh (1879). The following year Marsh (1880) figured the cranium in dorsal view, showing details of the endocranial cavity. Evidently the skull had been partially disarticulated, and in the illustrations (Fig. 2A, B, C) the medial and lateral surfaces of the quadrate, pterygoid, and quadratojugal were reversed. A corrected version of the illustration (Fig. 2F) appears in Marsh's (1896) "Dinosaurs of North America." In the mid-1880s Marsh had his preparators disarticulate all of the skull elements, a task they performed with remarkable skill considering the infancy of preparation techniques at that time. Each element was then illustrated in multiple views for a planned, but never completed, monograph on sauropod dinosaurs. Some of the figures were published more than 80 years later by Ostrom and McIntosh (1966), and the remainder are reproduced here for the first time. Eventually the skull was reassembled for exhibition, giving the original drawings an even greater importance.

Marsh obtained more cranial material from several quarries at Como Bluff during the years 1880–87, much of which consisted of disarticulated elements that were largely incomplete. Noteworthy among these collections were two skulls of *Camarasaurus* from Quarry 3, YPM 1907 and 1912 (Fig. 15, 29, 30, 33). YPM 1907 was apparently nearly complete and well preserved when found, but many of the fragile elements fragmented as a result of careless collecting. The importance of both skulls lies in the extraordinary perfection in which the tightly articulated elements of the braincase were separated by Marsh's preparators. Drawings of several of these, made under Marsh's direction, were published by Ostrom and McIntosh (1966:pl. 3) and are reproduced here (Fig. 27, 28, 32).

Also noteworthy, several partial skulls of *Camarasaurus* were collected about 6.5 km east of Como Bluff from Quarry 13 (Ostrom and McIntosh, 1966). Among these are some poorly preserved jaws belonging to the juvenile, holotypic skeleton of *Morosaurus lentus* (YPM 1910). Poor preservation, however, renders this material (Fig. 3) of little descriptive value. Of much greater importance is the anterior portion of a very large

skull, YPM 1911, found isolated and referred by Marsh (1883) to *Brontosaurus*. This specimen closely resembles *Camarasaurus* and was believed at one time to belong to that genus, but subsequent investigation by one of us (JSM) has shown that it may belong to *Brachiosaurus*.

During approximately 1882–83 Cope's collectors at Garden Park north of Canon City, Colorado, recovered cranial and jaw materials of two large *Camarasaurus* specimens (AMNH 5761; Fig. 2F, 4). This material was unpacked many years later, following Cope's death and its transferral to the American Museum of Natural History, and described and figured by Osborn and Mook (1921) as *Camarasaurus supremus*. Marsh also obtained material from a lower horizon at Garden Park which included a cranium he described (1889b) as "*Morosaurus*" *agilis* and which was later redescribed in detail by Gilmore (1907). It is unlikely that this specimen pertains to *Camarasaurus* and therefore will not be considered here. Marsh did receive a partial skull of *Camarasaurus* from Webster Park, Colorado, several years later, but incomplete preparation prevents it from being discussed here.

The first attempt to reconstruct the skull of *Morosaurus* (= *Camarasaurus*) was completed in 1905 by Adam Hermann under the direction of Osborn (1906). The skull, AMNH 467, was collected from the Bone Cabin Quarry northeast of Medicine Bow, Wyoming. Although the greater part of this specimen is preserved, it is badly crushed and somewhat scattered. Each element was disarticulated before the skull could be reassembled and described. The figure published by Osborn (1906) gives the shape and general proportions of the skull of *Camarasaurus* for the first time, but it still contains many inaccuracies. It was not possible at that time to identify all of the cranial elements, but some of those are determined here. Disarticulated braincases and jaw elements of several other skulls of *Camarasaurus* (AMNH 607, 611, 618, 657, 673, 677, 6126) were also collected from the Bone Cabin quarry.

Very large collections of sauropod material made during 1899–1906 by Carnegie Museum (now known as Carnegie Museum of Natural History) from quarries on Sheep Creek and the Red Fork of the Powder River in Wyoming

yielded few skull remains and only jaws of *Camarasaurus* (CM 113, 312) (McIntosh, 1981). However, the well-known Carnegie Museum of Natural History quarry at what is now Dinosaur National Monument north of Jensen, Utah, has yielded some of the finest skull material of *Camarasaurus*. Well-preserved upper and lower jaws of a large individual (CM 21751) were found in 1914. Two years later a large but imperfect skull was found associated with a disarticulated skeleton (CM 11393) that was first thought to be *Apatosaurus*. Although preparation revealed this specimen to be a large *Camarasaurus*, the skull was recatalogued CM 12020, and a cast of it was used in the mounted skeleton of *Apatosaurus louisae* (CM 3018) which was described by Gilmore (1936). This error has since been rectified (Berman and McIntosh, 1978; McIntosh, 1981).

In 1918 and 1919 two well-preserved, nearly complete skulls with mandibles were discovered as part of articulated skeletons CM 11373 (now USNM 13786) and CM 11338 at Dinosaur National Monument. The larger of the two skulls (USNM 13786) was somewhat crushed and distorted. The other skull (CM 11338), belonging to a very young individual, is only slightly distorted (Fig. 1D) and reveals almost all of the external dermal roof sutures. The lower jaws were firmly joined to the skull, although displaced slightly to the right. In order to expose the palate and the medial surfaces of both jaws the left was removed. The external features of the skull were first described by Gilmore (1925), who presented detailed figures in which errors in the earlier reconstruction by Osborn (1906) were corrected. About midway through the period of 1909–22 of the large scale excavation at the Dinosaur National Monument quarry by Carnegie Museum, two other skull specimens (CM 21732, 21702) were collected that consisted mainly of jaw materials.

When operations at the Dinosaur National Monument quarry were resumed in 1952 under the auspices of the National Park Service, the first specimen uncovered was a well-preserved, undistorted, and largely disarticulated skull and series of vertebrae of *Camarasaurus*. This specimen (DNM 28) was found in a soft layer of rock above the two sandstone layers that have yielded the great majority of specimens at the quarry. Because this

upper layer weathers quickly when exposed, the specimen was removed and prepared by the Monument's technicians F. (Tobe) Wilkins and F. McKnight under the direction of the late Park Paleontologist T. E. White. White (1958) published a detailed description of the braincase, commented on aspects of some of the other skull elements not available to Gilmore (1925), and also provided an excellent series of illustrations.

Two other skulls of *Camarasaurus* were found subsequently at Dinosaur National Monument. Both are articulated with a series of cervical vertebrae and have been worked out in relief on the quarry face as part of the Monument's permanent in situ exhibit. One of the skulls belongs with the greater part of a partially disarticulated skeleton preserved in the stratigraphically higher and more extensively quarried of the two bone-bearing sandstone layers. Because all but that portion of the layer immediately supporting the skeleton was excavated, the specimen appears on a strongly elevated area of the quarry face that is referred to as the "hump" by the quarry personnel. The skull (DNM 1009) has, therefore, become known as the "hump skull." The anterior end of the neck and skull lay beside the distal end of the right femur of this skeleton, necessitating the temporary removal of part of the femur by F. Wilkins in order to expose the skull. More recent additional preparation revealed the skull to be well preserved and therefore very important. Pressure from the femur at the time of deposition dislocated some of the elements of the right side of the skull, and the anterior part of the skull remains covered by matrix. The second skull (DNM 975) is articulated with a series of eight cervical vertebrae and lies some distance to the east of the hump skull. Because the second skull is positioned on the cliff, it is commonly referred to as the "cliff skull." The right side and much of the posterior and dorsal aspects have been exposed. Most of the skull is articulated, but the right quadrate, quadratojugal, and a number of the palatal elements have been displaced ventrally. Several of these bones have been lost, whereas others (right pterygoid and palatine) have been removed and fully prepared. The articulated dentary, surangular, and angular, and the disarticulated prearticular and splenial of the right mandible were displaced from the skull and

were removed from the quarry for preparation and have provided details about the relationships of the lower jaw elements. The left mandible is articulated with the skull, and its prepared medial surface clearly reveals the sutural pattern. The excellent preservation of the skull, together with its well-defined sutures, has provided invaluable information in this study.

The latest and one of the most important discoveries of skull materials referable to *Camarasaurus* was made at the Cleveland-Lloyd Dinosaur Quarry east of Cleveland, Emery County, Utah, by a University of Utah field party under the direction of J. H. Madsen (Madsen and Stokes, 1972). This locality, most famous for its spectacular remains of *Allosaurus* (Madsen, 1976), has yielded disarticulated and largely scattered skeletons of at least five different sauropods, only three of which can be definitely assigned to *Camarasaurus*. Not only are the skeletons disarticulated but, with the exception of the braincases, so are the skulls. Of the five braincases, four (UUVP 3568, 4286, 10070, 10795) were found in the same general part of the quarry and were all variously associated with other elements of the skull. The fifth braincase (UUVP 5684), which is assigned to *Camarasaurus*, was displaced from the other four, but is incomplete and badly eroded. Other elements of the skull may have been associated with UUVP 5684 but, as their positions in the quarry provide no help in determining associations, they could also represent more than one individual. Some of the other disarticulated cranial elements have been assigned separate catalogue numbers. This was done even though three of the four braincases from the same part of the quarry were sufficiently separated from each other to allow their fairly certain association with many of the other disarticulated bones. It is unfortunate that definite associations could not be made, since the resulting skull-bone assemblages exhibit subtle differences from each other, making it possible to recognize two aberrant skulls that may pertain to camarasaurid taxa other than *Camarasaurus*. These two skulls have a definite *Camarasaurus*-like structure that is similar to, for example, those of *Camarasaurus*, *Brachiosaurus*, or *Euhelopus* and are, therefore, easily distinguishable from the skulls of such diplodocids as *Diplodocus*, *Apatosaurus*, or *Dicraeosaurus*.

Although the bulk of the postcranial sauropod materials from the Cleveland-Lloyd quarry can be assigned to *Camarasaurus*, at least two other sauropod taxa have been recognized. The presence of *Barosaurus* is clearly indicated by a series of caudal vertebrae, a pair of ischia, and other elements, but this genus is a diplodocid (McIntosh and Berman, 1975). *Haplocanthosaurus* also appears to be represented by three caudals, an ischium, and other elements. The skull of this genus is not known, but, like other cetiosaurids, it would be expected to possess broad, spatulate teeth of the general type found in *Camarasaurus*. On the other hand, considering the pronounced differences between the postcrania of these two genera, their skulls would be expected to exhibit much greater differences than those found among the camarasaur skulls of the Cleveland-Lloyd quarry. Yet, it is known that, unlike the condition found in most other vertebrate groups, the skulls of sauropod genera tend to be less diagnostic than the vertebrae, as for example in *Diplodocus* and *Apatosaurus* (Berman and McIntosh, 1978). Thus, it is possible that one of the two aberrant Cleveland-Lloyd skulls may indeed pertain to *Haplocanthosaurus*. It is important to emphasize here that, of the four braincases with associated skull elements, two cannot be distinguished from that of *Camarasaurus*. As an example, they are indistinguishable from the seven skulls of *Camarasaurus* from Dinosaur National Monument, which incidentally do not exhibit the same range of variation as the Cleveland-Lloyd skulls. Further, the two aberrant Cleveland-Lloyd skull-bone assemblages differ more strongly from one another than either does from those assigned to *Camarasaurus*. Thus, if the differences between the four skulls are not due to sexual or individual variation, the only alternative explanation would be that three camarasaurid genera, including *Camarasaurus*, are represented in the Cleveland-Lloyd quarry.

Of the six well-established Morrison sauropod genera, the only one that could possibly be represented by one of the two aberrant, *Camarasaurus*-like skull-bone assemblages is *Brachiosaurus*. However, the structure of the lacrimal in one of the aberrant skulls (UUVP 10795) and the braincase in the other (UUVP 3568 and associated elements) would seem to preclude this assignment.

That a seventh, as yet undescribed, Morrison sauropod with a *Camarasaurus*-like skull could exist seems quite unlikely. Thus, the dilemma arises as to how to resolve the question of the systematics of the two aberrant, *Camarasaurus*-like skull-bone assemblages. Clearly, assigning one or the other to *Haplocanthosaurus* would be pure speculation. It was decided that the least confusing solution would be to refer to the two aberrant skull assemblages as *Camarasaurus*-like skull *a* (UUVP 10795) and *Camarasaurus*-like skull *b* (UUVP 3568 and associated elements). Complete listings of their component elements are given in Appen-

dix 1. In the description below, differences between the individual elements of the two aberrant *Camarasaurus*-like skulls and those of a typical specimen of *Camarasaurus* are noted. Thereby, the question of whether the differences have taxonomic significance or merely represent individual variation is postponed until articulated material is eventually recovered, while at the same time bringing to light what might be potentially important data. The primary importance of the Cleveland-Lloyd quarry collection is the opportunity to study isolated elements in all views.

DESCRIPTION

EXTERNAL SKULL FENESTRATION

Gilmore (1925) provided a detailed description of the external openings of the skull based on *Camarasaurus* CM 11338, and only a brief account is necessary here. Three of the five pairs of major openings on the lateral and dorsal surfaces of the skull, the external nares, orbits, and infratemporal fenestrae, are very large and subequal in size; the antorbital and supratemporal fenestrae are considerably smaller. The oval-shaped external naris is bounded anteriorly by the premaxilla, ventrally and posteriorly by the maxilla, and dorsally by the nasal. The orbit has the general shape of a broad, inverted teardrop. It is bounded dorsally by the prefrontal, frontal, and postorbital, posteriorly by the postorbital and jugal, and anteriorly by the lacrimal. The orbit contains a ring of scleral ossicles, as shown in CM 11338 and USNM 13786 (Fig. 1D). In the incorrectly restored skull AMNH 467 (Fig. 1E) the orbit is twice actual size. When the lacrimal was restored it was positioned too far anteriorly, resulting in expansion of the orbit at the expense of the antorbital fenestra. The elements of the dorsal margin of the orbit, particularly the postorbital, were also restored incorrectly, further distorting and enlarging the dimensions of the orbit. The infratemporal fenestra is subtriangular in outline, with the long axis directed 30° posteroventrally from the vertical. This opening lies posteroventral to the orbit, rather than directly posterior as it was restored in AMNH 467 (Fig. 1E). The fenestra is

bordered by the squamosal dorsally, the postorbital and jugal anteriorly, the jugal and quadratojugal ventrally, and the quadratojugal and squamosal posteriorly. The quadrate is excluded from the posterior bar of the infratemporal fenestra. The smallest of the major paired external openings, the supratemporal fenestra, lies posterodorsal to the orbit and faces dorsally. It is an elongate oval in outline, with the long axis oriented transversely to the skull midline. The border is formed by the postorbital laterally, the postorbital and parietal anteriorly, the parietal medially, and the parietal and squamosal posteriorly.

The circular foramen magnum is bounded by the supraoccipital dorsally, the exoccipitals laterally, and the basioccipital ventrally. A pair of very small, ventrolaterally elongate posttemporal fenestrae are located near the lateral margins of the occiput. They are bounded dorsolaterally by the squamosal and parietal and ventromedially by the paroccipital process of the opisthotic. The questionable occurrence of a pineal opening is discussed in the descriptions of the parietal and frontal, and the palatal fenestrae are described with the descriptions of the palate. There are no major external fenestrae in the mandible.

SKULL ROOF BONES

Premaxilla.—Premaxillae from the Como Bluff area include a left of the holotype of *C. lentus* (YPM 1910) and a right of USNM 7759, both incomplete, and a fragmentary pair of YPM 1907.

The premaxillae found with the restored skull AMNH 467 are nearly complete, as are those of CM 11338, USNM 13786, and DNM 975. Among the most informative premaxillae are the complete and well-preserved pair of the largely disarticulated skull DNM 28. Also from Dinosaur National Monument are two nearly complete elements, CM 21751 and 11969, and an extremely small right premaxilla (DNM 3699) exposed on the quarry face. Similarly, from the Cleveland-Lloyd quarry are well-preserved, disarticulated premaxillae UUVP 3999 (r) (Fig. 7A–D) and 10062 (l) (Fig. 7E–H), as well as several incomplete specimens UUVP 1223 (r), 5645 (r) (Fig. 7I–L), 4008 (l), and some fragments (UUVP 3859, 4323, 3887). Lastly, there are two large, incomplete premaxillae, YPM 619 from Webster Park, Colorado, and AMNH 677 (r) from Bone Cabin quarry.

The robust body of the premaxilla (Fig. 7, 9) is subrectangular in lateral view, giving the skull a blunt, bulldog-like muzzle in lateral view. The median symphysis is a very broad, flattened surface. In lateral view the anterior margin of the premaxilla rises nearly vertically from the dental margin to about the ventral level of the naris, then curves smoothly posterodorsally. The nasal or dorsal process of the premaxilla is positioned in a step-like manner a short distance posterior from the anterior margin of the body of the element. This transversely thin, blade-like process tapers to a distal point as it curves posterodorsally to form more than half of the internasal bar. The distal end of the nasal process inserts into a dorsal groove on the anterior end of the premaxillary process of the nasal. There are alveoli for four large teeth in the premaxilla. Four small, elliptical nutrient foramina for branches of the maxillary artery and the superior alveolar nerve exit in a horizontal groove above the tooth row on the medial surface. Just below the foramina there is a step-like narrowing of the premaxilla of about a millimeter or more, so that the foramina face ventrally.

The premaxilla and maxilla articulate mainly by a wide, flat abutting contact that extends from the ventral skull margin dorsally to a level a short distance below the base of the nasal process. This union is strengthened by two maxillary processes of the premaxilla. A short, broadly rounded ventral maxillary process overlaps the anterior margin of

the medial surface of the maxilla just above the tooth row. A dorsal maxillary process consists of two short, fragile, tongue-like components that project directly posteriorly from the base of the nasal process just above the block-like portion of the premaxilla and are positioned one closely above the other. The more ventral, or internal, component inserts into a groove on the medial surface of the anterodorsal plate of the maxilla (see below). The internal components of the paired premaxillae join medially to form an anteroposterior slot that supports the anterior ends of the vomers. The more dorsal, or external, component of the dorsal maxillary process lies just below the ventral margin of the naris, overlapping laterally the anterodorsal plate of the maxilla in a nearly vertical, squamous contact.

The block-like body of the premaxilla in *Brachiosaurus* closely resembles that in *Camarasaurus*, but the nasal process is very different. Instead of rising nearly vertically above the body of the element, it is directed almost straight back over the maxilla. After extending to a level nearly twice the length of the body of the premaxilla, the nasal process turns dorsally as it narrows considerably. The dorsal curvature of the process is more abrupt than in *Camarasaurus*, as is the posterior curvature at the distal end of the process just before it joins the nasal. The premaxilla in *Euhelelopus* is very similar to that of *Camarasaurus*, the main difference being that it forms a less blunt muzzle. In the diplodocids *Diplodocus*, *Barosaurus* (from Tendaguru), *Dicraeosaurus*, and *Nemegtosaurus* the shape of the premaxilla is different from that in *Camarasaurus*. The body of the bone is much narrower, and the nasal process extends posterodorsally as a narrow process without any flexure and has a nearly straight union with the maxilla. Distally the nasal process ends abruptly at the anterior margin of the naris without reaching the nasal, thereby leaving the external naris as a single, unpaired opening. In contrast to *Camarasaurus* the snout of the prosauropod *Plateosaurus* is much narrower in width, the premaxilla contains five teeth, and its nasal process projects strongly posteriorly. In *Plateosaurus* the premaxilla has only one maxillary process, but it is much stouter and longer than either of the two processes in *Camarasaurus*. Lastly, the entire snout of *Plateo-*

saurus is much narrower dorsoventrally, with the premaxillae having a much broader symphyseal union.

Maxilla.—The stoutly constructed maxilla is not only the largest and one of the most commonly preserved elements of the skull of *Camarasaurus*, but also one of the most diagnostic. Often found disarticulated, most of the earliest collected maxillae were variously incomplete, such as YPM 1905 (p) (Fig. 8), 1907 (p), 1910 (p), and 619, AMNH 611 (p), 673, and 5761, USNM 7944, and CM 113 and 21702. The nearly perfectly preserved maxillae of DNM 28 (Fig. 9, 10) allowed White (1958) to describe briefly the medial surface of the bone; the lateral surfaces were at that time encased in plaster. Of the four well-preserved, disarticulated maxillae UUVP 1859 (l), 1860 (r), 3454 (l), 4005 (l) from the Cleveland-Lloyd quarry that allow a detailed description of the bone in all views, the first is figured here (Fig. 10). The right maxilla of DNM 975 is complete, but only the lateral surface has been completely exposed. Important details of the lateral surface are also gained from maxillae in the articulated skulls CM 11338 and 12020 (=11393), USNM 13786, and AMNH 467, although their contacts with neighboring elements are often indistinct. A right maxilla, DNM 4257, is exposed in lateral view on the quarry face at Dinosaur National Monument.

The maxilla in general consists of a stoutly constructed main body from which an ascending nasal process and a dorsal plate arise from the anterior two-fifths of its dorsal surface and a smaller triangular plate from its posterior end. The long, slender nasal process expands somewhat as it extends posterodorsally. The noticeably expanded distal end of the process is overlapped along the anterior margin of its lateral surface by a descending lateral process of the nasal. The area of this union in turn articulates with an anteriorly facing, L-shaped trough formed by two laminae of the dorsal end of the lacrimal. The smaller of the two laminae extends onto the lateral surface of the nasal process to buttress the maxilla–nasal contact, whereas the larger of the two laminae contacts the posterior half of the medial surface of approximately the upper half of the nasal process of the maxilla.

Extending anteriorly from the base of the nasal

process and the dorsal surface of the palatine shelf is a prominent, blunt, premaxillary process. At levels just above and below the premaxillary process are shallow grooves on the medial surface of the maxilla that receive the paired components of the dorsal maxillary process of the premaxilla and strongly lock the two elements together. The maxillary and premaxillary processes of the premaxilla and maxilla, respectively, join with their counterparts along the midline to form the floor of the nares. Just medial to the outer margin of the anterior end of the dorsal surface of the main body lies a rather deep excavation, at the bottom of which lies a large foramen of unknown function, the anterior maxillary foramen. A small, dorsally directed, triangular lacrimal process at the posterodorsal corner of the main body of the maxilla inserts into the grooved, expanded ventral end of the lacrimal in a joint which may have permitted some movement. Below this process a broad, deep sutural scar for the jugal borders most of the posterior margin of the medial surface of the body of the maxilla. The posteroventral corner of the body of the maxilla unites with the anterior end of the quadratojugal, excluding the jugal from the ventral margin of the skull.

The tooth row occupies almost 75% of the ventral margin of the maxilla. The number of teeth is slightly variable, there being ten in DNM 28 and USNM 13786, nine in the Cleveland-Lloyd specimens, and nine in the right and eight in the left of CM 11338. The tightly packed alveoli, most visible in medial view of the maxilla, are slightly oval with a greater transverse width, and the series decreases in size posteriorly. The alveolar groove just above the tooth row is continuous with that of the premaxilla. Above each alveolus is a dorsally-directed, elongate, oval nutrient foramen. A pronounced palatine shelf extends parallel to and just above the alveolar groove. At the posterior end of the shelf are two adjacent sutural scars, a smaller anterior scar for the palatine and a larger, oval posterior scar for the ectopterygoid. On the dorsal surface of the shelf is a series of three or four anterodorsally-directed foramina of uncertain function that extends from immediately behind the nasal process posteriorly to a level above the ectopterygoid scar.

The maxilla in *Brachiosaurus*, although gener-

ally similar to those of other sauropod genera, differs in being much more elongate and giving the skull a protruding snout rather than the bulldog-like muzzle of *Camarasaurus*. In *Brachiosaurus* the maxilla possesses 11 teeth. The nasal process arises posterior to the midlength of the bone, and the anterior dorsal plate has a much different shape. The maxilla has a much reduced contact with the jugal, and, because the base of the lacrimal makes a much broader contact with the jugal, its more anterior contact with the maxilla is greatly reduced. The maxilla in *Euhelopus* is similar to that in *Camarasaurus* in possessing nine teeth. In a juvenile specimen of *Pleurocoelus* (USNM 5607) the maxilla, although incompletely known, is also very similar to that in *Camarasaurus*, particularly in the structure of the premaxillary process. The structure of the maxilla in diplodocids is strikingly different in that the teeth are confined to the extreme anterior part of the jaw, and the nares are displaced far dorsally. The nasal process is much broader in *Diplodocus*, but apparently not in *Nemegtosaurus*. The maxilla in *Diplodocus* is very thin throughout its extent, and the more pronounced palatine shelf projects from a much higher level on the medial surface, with the ectopterygoid and palatine articulating with the shelf ventrally rather than medially. In contrast to *Camarasaurus* the anterior maxillary foramen in *Diplodocus* is larger and occupies a truly superficial position on the lateral surface of the snout. The position of the anterior maxillary foramen in *Nemegtosaurus* is the same as that in *Diplodocus* except for being divided into two much smaller openings. Although the maxillae of *Barosaurus* from Tendaguru and *Dicraeosaurus* are not complete enough to allow a detailed comparison, they are clearly diplodocid rather than camarasaurid. The maxilla in *Plateosaurus* is very different from that in *Camarasaurus* in being relatively much longer and having 20 or more alveoli. The nasal process is much broader and arises from a more posterior level, but still anterior to the midlength, as a result of relative lengthening of the posterior portion of the maxilla. The palatine shelf is more like that in *Diplodocus* than *Camarasaurus*.

Nasal.—The external surface of the nasal is well-preserved in the articulated skulls CM 11338, AMNH 467, and USNM 13786 (right only), and

the partly disarticulated skull DNM 28 (Fig. 12A–D). Of three incomplete, isolated nasals from the Cleveland-Lloyd quarry, the most complete and useful is UUVP 3963 (r) (Fig. 12E–G), which lacks only the end of the somewhat distorted lacrimal process, the tip of the anterior premaxillary process, and a small part of the posterior margin. The other two nasals, UUVP 5644 and 5108 (both lefts), are larger and less complete, lacking much of their slender, premaxillary processes, but the latter is particularly useful in possessing a complete lateral process. Lastly, the sutural contacts of the nasal in DNM 975 (Fig. 6B, D) are exceptionally clear.

The nasal is a thin, arcuate, plate-like bone that is gently arched dorsally. A small fracture in the skull roof of CM 11338 misled Gilmore (1925) to incorrectly interpret the nasal–frontal suture as a simple transverse contact. As is clearly seen in DNM 975 (Fig. 6B), although the greater medial portion of the contact is transversely straight, the posterolateral corner of the nasal is directed posteriorly as a blunt, triangular, tab-like process that contacts the prefrontal laterally and overlaps the frontal dorsally. Just anterior to this process is a strongly downturned, slender but strongly built, wing-like lateral process of the nasal whose lateral surface is ornamented by shallow grooves. It inserts into a deep groove on the anterior margin of the lateral surface of the lacrimal and extends ventrally to just above the lacrimal foramen. The distal end of the nasal process of the maxilla abuts against the anterior surface of the lateral process of the nasal, and thus all but the lateral surface of the lateral process is overlapped (Fig. 6B). Anteriorly the nasal quickly narrows as its lateral border smoothly arches medially to form the dorsal rim of the naris. The slender, greatly attenuated premaxillary process is separated from its mate by a narrow gap and overlaps dorsally the equally slender nasal process of the premaxilla.

The nasal has been described in only two other Upper Jurassic sauropods, *Brachiosaurus* and *Diplodocus*. The nasal of *Brachiosaurus* exhibits a general resemblance to that in *Camarasaurus*. However its anterior premaxillary process, which separates the nares, is much more slender and appears to be arched much higher dorsally, an illusion caused in part by the much more elongate

snout of *Brachiosaurus*. The contact with the frontal is straighter than in *Camarasaurus*. As a result of the extraordinary development of the snout in *Diplodocus*, the nasal is reduced to a transversely elongate, subrectangular plate. The anterior border of each nasal is slightly concave, so that together the paired elements produce only a nubbin-like internasal projection. Further, in *Diplodocus* the nasal-frontal suture is sinuous, and the contact between the lacrimal process of the nasal and the nasal process of the maxilla is much simpler than that in *Camarasaurus* and *Brachiosaurus*. In *Plateosaurus* the premaxillary and lateral processes are shorter, and the posterior plate-like area is much more expanded.

Prefrontal.—Prefrontals are present in the articulated skulls CM 11338 and USNM 13786, and the largely disarticulated skull DNM 28 (Fig. 22). In DNM 975 the outer surface of the right prefrontal shows very clearly the complex sutural contacts of this element with the nasal and lacrimal (Fig. 6D). Prefrontals are either firmly sutured or fused to the crania of AMNH 973, CM 11969, and UVP 3568 (left side only). Finally and very importantly, the Cleveland-Lloyd collection contains two complete, disarticulated prefrontals, UVP 5036 (l) and 5126 (r).

The prefrontal (Fig. 6D, 13, 22, 24, 25) is a relatively small, stoutly built element with an elliptical exposure that forms the anterior portion of the thickened, rugose dorsal rim of the orbit. It is block-like with an anteroposterior length equal to one and a half to two times its transverse width and a vertical thickness nearly equal to its maximum width. Anteriorly a short lacrimal process curves ventrally around the anterodorsal rim of the orbit to abut against the posterior face of the dorsal end of the lacrimal. The prefrontal joins the nasal medially and the frontal posteriorly.

The prefrontal in *Brachiosaurus* closely resembles that in *Camarasaurus*. Even the prefrontals in *Diplodocus* and *Nemegtosaurus* closely resemble that in *Camarasaurus*, although it is more elongate in the former. In *Antarctosaurus* the prefrontal is distinctively broader than that in *Camarasaurus*. The prefrontal of the prosauropod *Plateosaurus* differs considerably in being much thinner and relatively larger, and possessing a very prominent ventral lacrimal process.

Frontal.—Frontals are preserved in all the articulated skulls and braincases discussed in this study (Fig. 22–26) except AMNH 5761 and 6126. Most useful are the nearly complete and disarticulated elements from Como Bluff, YPM 1905, 1907, and 1912 (Fig. 14, 15). Detailed drawings of the frontal of YPM 1905, the most complete, were made under Marsh's direction while the skull was disarticulated and are published here for the first time (Fig. 14A–D). Details of the anterior margin of the frontal not seen in the Yale Peabody Museum specimens are well exhibited in DNM 975 (Fig. 6A, B).

The frontals have a finely interdigitating median suture, and together form a thick, subrectangular plate. In dorsal view the lateral margin of the frontal curves very slightly posterolaterally as it forms the rounded, rugose, dorsal orbital rim and the medial half of the posterior wall of the orbit. The frontal-parietal suture is a nearly straight, transverse contact for much of its length, curving slightly anterolaterally as it skirts the upper end of the supratemporal fossa. Laterally from this point the posterior border of the frontal is continued in contact with the postorbital. The frontal-nasal suture is a transversely straight abutment except for its extreme lateral end, where it is overlapped dorsally by the posteriorly directed, tab-like process of the posterolateral corner of the nasal. At the level of the posterior extent of the tab-like process of the nasal the margin of the frontal curves anterolaterally in contact with the prefrontal. The dorsal surface of the frontal is nearly flat, but the ventral surface exhibits some relief, as shown most clearly by the articulated frontal-parietal in YPM 1905 from Como Bluff (Fig. 14). Most noticeable is a rugose, band-like sutural scar for the laterosphenoid and orbitosphenoid that is coarsely marked by transverse ridges. It begins anteriorly at the midline suture at a level just posterior to the midlength of the frontal and increases in width as it curves smoothly posteriorly to traverse both the frontal and parietal. From near the anterior end of the braincase scar a sharp ridge extends anterolaterally across the frontal and the adjoining prefrontal to the orbital rim. This ridge separates the posterior orbital cavity from the anterior nasal region.

The exact nature of the midline juncture of the

frontals and parietals has been the subject of controversy (Marsh, 1879; White 1958). The paratype of *Morosaurus* (= *Camarasaurus*) *grandis*, YPM 1905, has a large circular opening at this point (Fig. 2A), which was interpreted by Marsh (1879) as a pineal foramen. Many of the *Camarasaurus* crania found since that report apparently also have this feature, including AMNH 467 and 973, and UVP 3568. On the other hand, of those crania from Dinosaur National Monument, CM 11338, 11969, and USNM 13786 definitely lack a pineal-like foramen, whereas DNM 975 apparently lacks one and DNM 28 exhibits some indication of a similar foramen in the pineal area. White (1958) described the foramen in several skulls and apparently believed it to be typical of the genus. He overlooked, however, Gilmore's (1925) inability to find it in the excellently preserved skull of CM 11338. Several explanations are plausible for these contrasting descriptions: 1) the foramen occurs in juveniles, but is covered by a thin layer of bone in more mature individuals; 2) no foramen exists and a very thin bone covering the pineal organ is lost in many specimens due to poor preservation or preparation; 3) the openings in the specimens examined in this study exist as vestiges of the pineal opening and as such are not consistently developed and may also be misinterpreted due to the vagaries of preservation and preparation; and 4) two different species are indicated. The first of these explanations appears unlikely, since CM 11338, which lacks the foramen, is obviously the least mature of all of the specimens. The second explanation is probably the most likely, but an examination of all of the skulls suggests that some of the openings are genuine. With regard to the fourth explanation, it can be noted that *C. grandis* from the Como Bluff and Bone Cabin quarries possesses the foramen, whereas the referred specimens of *C. lentus* (perhaps identical with *C. supremus*) from Dinosaur National Monument lack it. The frontoparietal region of the holotype of *C. lentus*, YPM 1910, is not preserved. This specimen was reported (Marsh, 1889b) as having been collected from Quarry 13 at Como Bluff, but this quarry is about four miles east of the bluff proper. No other cranial evidence for the fourth possibility can be noted, but there is evidence in the presacral vertebrae for recognition of two species.

Frontal bones exhibit little variation among the sauropods. Those in *Brachiosaurus* and *Camarasaurus* are nearly identical, differing mainly in the anterior margin being straighter in the former.

Parietal.—The paired parietals and frontals are always so tightly sutured together that they are never found disarticulated. For this reason all of the specimens listed above as having the frontal represented also include the parietal (Fig. 14, 22–26); the transverse, slightly sinuous frontal-parietal suture is clearly discernible in several specimens (Fig. 6A, B; Fig. 25C). The paired parietals make only a very narrow contribution to the skull roof along the occipital margin. Laterally they bifurcate into wing-like processes that form the dorsomedial margins of the supratemporal fenestrae. A vertical, slender, wing-like anterolateral process extends a short distance along the anterior wall of the supratemporal fenestra, uniting distally with the postorbital and excluding the frontal from the rim of the fenestra. A more vertically expanded, wing-like posterolateral process of the parietal forms the medial half of the posterior wall of the supratemporal fenestra, contacting the squamosal distally, as well as having an extensive occipital exposure. The central portion of the parietal slopes slightly posterovertrally to overlie the dorsal surface of the prootic and contact the dorsal margin of the supraoccipital on the occiput.

The parietals in *Brachiosaurus* resemble those in *Camarasaurus*, but are somewhat arched centrally. In contrast, the parietals in *Diplodocus* form a broad, shallow depression on the skull roof. In *Antarctosaurus* the portion of the parietals exposed on the skull roof has a greater anteroposterior length than those of other sauropods. The parietals in *Plateosaurus* are much more sauropod-like than the frontals, although the lateral wing-like processes diverge much more from one another because the bone is relatively much longer.

Lacrima.—Lacrimal bones are preserved in the articulated skulls CM 11338, USNM 13786, and DNM 975 (only right side exposed), as well as disarticulated specimens DNM 28 (r), UVP 3371 (r), and in the *Camarasaurus*-like skull a UVP 10795 (r).

The long, narrow lacrimal is vertically oriented,

although slightly bowed anteriorly, and undoubtedly serves as a brace between the jaw and the skull roof (Fig. 6D–E, 10, 16). The ventral half of the lacrimal is blade-like, with a greater antero-posterior than transverse width. The medial surface of its ventral foot-like expanded end is grooved to receive the lacrimal process of the maxilla. The posterior half of the lateral surface of the expanded ventral process is, in turn, overlapped by the jugal. The upper half of the lacrimal increases in transverse width dorsally until just before its terminal union with the prefrontal, where it decreases abruptly in width. The prefrontal slightly overhangs the dorsal end of the lacrimal. A thin, vertical lamina projects anteriorly from the dorsal half of the lateral surface of the lacrimal, forming a groove which receives the nasal process of the maxilla and the wing-like lateral process of the nasal. Just behind the anteriorly directed lamina the posterior surface of the body of the lacrimal is pierced by a vertically elliptical lacrimal foramen.

The lacrimal in *Brachiosaurus* is similar to that in *Camarasaurus*, but has a greater contact with the jugal, although still having a small anterior contact with the maxilla. In *Diplodocus* the lacrimal is somewhat broader, thicker, and shorter. As shown in the lateral views of the articulated skulls CM 11161, USNM 2673, and AMNH 969, its ventral articulation is solely with the jugal, although the possibility of a medial contact with the maxilla cannot be ruled out. The lacrimal in *Dicraeosaurus* and *Nemegtosaurus* is more stoutly constructed than that in *Camarasaurus*. The lacrimal in *Plateosaurus* is relatively much larger and somewhat simpler in structure, and above its very broad lower portion it narrows before expanding rapidly dorsally. Further, the dorsal end is twisted 90° about its long axis and makes a large contribution to the skull roof.

Jugal.—Knowledge of the jugal of *Camarasaurus* has heretofore been limited to brief descriptions of its external surface by Gilmore (1925) and White (1958), with that of the latter, however, being supplemented by a detailed illustration of the medial surface. In addition to the disarticulated, nearly complete jugals in the *Camarasaurus*-like skull *a* from the Cleveland-Lloyd quarry (UUVP 10795, Fig. 17), the removal of the right quadratojugal in DNM 975 reveals a well-

preserved jugal exhibiting detailed features (Fig. 6C). Thus, it can be determined from DNM 975 that the processes of the jugal which articulated with the postorbital and quadratojugal are incomplete in DNM 28 (Fig. 9, 10, 17).

The jugal is greatly reduced in all sauropods, but to the greatest extent in *Camarasaurus*, where it is completely excluded from the lower margin of the skull by a contact between the maxilla and quadratojugal. In general the jugal is V-shaped, but only in DNM 975 are both limbs or processes of the jugal complete and clearly discernible (Fig. 6C). The expanded anteroventral angle of the bone is set firmly in a slot on the lateral surface of the posterior margin of the maxilla. In DNM 975 two small, thin processes at the maxillary contact project anteriorly onto the lateral surface of the maxilla, a feature whose development may be related to age. A posteroventral or quadratojugal process is slender and quite elongated. It extends along the dorsomedial surface of about the anterior third of the anterior process of the quadratojugal that forms the posterior half of the ventral arch of the infratemporal fenestra. The full extent of the quadratojugal process of the jugal may be hidden from lateral view by the quadratojugal. Nearly the distal half of a somewhat broader posterodorsal or postorbital process of the jugal extends along the posteroventral margin of the anteroventral or jugal process of the postorbital in a very oblique suture. The postorbital process of the jugal extends for nearly three-fifths of the anterodorsal margin of the infratemporal fenestra.

A distinctive character of *Camarasaurus* is the reduction of the contact between the jugal and lacrimal, as is clearly shown in both CM 11338 and DNM 28 (Fig. 6C, 9, 10). In contrast to *Camarasaurus*, the jugal in *Plateosaurus* is triradiate, with broad processes contacting the maxilla, postorbital, and quadratojugal. It also makes a major contribution to the ventral rim of the skull, and the lacrimal and ectopterygoid contact the jugal rather than the maxilla. The jugal in *Brachiosaurus* represents an intermediate condition between those in *Plateosaurus* and *Camarasaurus*. It is very similar in shape and almost as large relatively as that in *Plateosaurus*. The jugal of *Brachiosaurus* barely reaches the ventral rim of the skull, and, as mentioned previously, although

the ventral end of the lacrimal contacts mainly the jugal, the ectopterygoid contacts the posterior end of the medial surface of the maxilla. The jugal in *Diplodocus* is smaller than that in *Brachiosaurus*, but it is still appreciably larger than that in *Camarasaurus*. It is essentially triradiate; the quadratojugal and postorbital processes are greatly reduced, and a narrow dorsal process extends along the ventral half of the anterior margin of the lacrimal. The maxilla and lacrimal are widely separated by the jugal. The jugal in *Nemegtosaurus* is identical to that in *Diplodocus* except in being somewhat smaller.

Postorbital.—The postorbital is represented in numerous skulls from Como Bluff (YPM 1905, 1907, 1912), and Dinosaur National Monument (CM 11338, 11969; USNM 13786; DNM 28, 975), as well as by isolated elements from the Cleveland-Lloyd quarry (UUVP 2300 [r], 3359 [l], 5434 [r], 10795 [p]) and from several quarries in southeastern Wyoming (AMNH 467, CM 113). Except in articulated skulls the anteroventral jugal process is typically incomplete. The disarticulated postorbital UUVP 5434, however, is nearly complete, and knowledge of missing areas can be supplemented by DNM 975 and CM 11338. Although it is likely that the postorbital actually represents the fused postorbital and postfrontal, no trace of a suture has been reported in any saurischian skull, even in juvenile specimens. For this reason the postorbital is referred to as if it were a single element. Huene (1914:fig. 8), however, has figured several sauropod crania in which a suture demarks the area generally considered the orbital portion of the parietal as the postfrontal. No other author, including us, concurs with this interpretation.

The postorbital (Fig. 6A, 6C, 18) is triradiate. A short, posterior process tapers distally to a point which inserts into a deep, V-shaped cleft on the lateral surface of the squamosal. The lateral surface of the process appears to be deeply excavated in UUVP 5434 (Fig. 18E, F). A thick, medially expanded, laterally rugose, anterodorsal process forms the wall separating the orbit and supratemporal fenestra. A deep cleft on the orbital margin of the distal end of the process receives the posterolateral corner of the frontal. The medial expansion of the anterodorsal process extends

nearly to the medial wall of the supratemporal fenestra, contacting the short anterolateral, wing-like process of the parietal in a vertical suture. A third, greatly attenuated, anteroventral process extends essentially the entire length of the boundary between the orbit and infratemporal fenestra. The process is triangular in cross section with a pronounced medial ridge that is continuous with the wing-like crista antotica of the laterosphenoid. At this level the transverse width of the process is much greater than its anteroposterior width, but narrows markedly distally.

The postorbital in *Brachiosaurus* is similar to that in *Camarasaurus* except for the anteroventral process being more slender. *Euhelopus* also has a postorbital similar to that in *Camarasaurus*, but the medial expansion that contacts the anterolateral process of the parietal to form the anterior wall of the supratemporal is very short and projects from the juncture of the anterodorsal and anteroventral processes. In *Diplodocus* the bone is more massive, particularly the anteroventral process which has a rather simple transverse contact with the jugal. In contrast to *Camarasaurus* the anteroventral process in *Nemegtosaurus* is very slender, and the posterior process has a simple, vertical contact with the squamosal. From what can be ascertained from the incomplete postorbital in *Dicraeosaurus* the anteroventral process is also slender. The anteroventral process is not known in *Antarctosaurus*, but the orbital rim of the postorbital appears to be much narrower than in *Camarasaurus*. The postorbital in *Plateosaurus* is different from that in *Camarasaurus* in having a shorter anteroventral process, a thinner anterodorsal process, and a considerably longer and more slender posterior process.

Quadratojugal.—The external surface of the quadratojugal is exposed in the articulated skulls AMNH 467 (l), YPM 1905 (Fig. 19A–D), CM 11338, and USNM 13786. The disarticulated right quadratojugal of DNM 975 has been removed and prepared (Fig. 19H–J). The Cleveland-Lloyd quarry has yielded two complete, disarticulated left quadratojugals, UUVP 3293 and 10063, and those of the largely disarticulated skull DNM 28 are complete and freed (Fig. 19E–G).

In lateral view the quadratojugal appears as a narrow, L-shaped plate whose vertical or dorsal

process is much shorter than the horizontal or anterior process. The union of the processes is slightly expanded to form an abrupt right angle. A ventrally tapering concavity along the anterior margin of the lateral surface of the dorsal process received the squamosal. In lateral view their contact is a nearly vertical, oblique suture that excludes the quadrate from the external surface of the skull; this is best exemplified on the left side of USNM 13786 and the right side of CM 11338 (Fig. 1C). The dorsal process is slightly bowed laterally, and its medial surface laterally overlaps the quadrate. The ventral margin of the horizontal anterior process is straight, whereas the dorsal margin is gently concave, so that the process gradually expands distally. The expanded anterior end overlaps the lateral surface of the distal end of the posteroventral process of the jugal to contact narrowly the posterior end of the maxilla. A shallow concavity along the dorsal margin of the medial surface of the distal half of the anterior process of the quadratojugal contacted the posteroventral corner of the body of the maxilla.

The quadratojugal in *Brachiosaurus* is similar to that in *Camarasaurus* except for the dorsal process being more slender and the anterior process being slightly broader. A much larger jugal overlaps the dorsal margin of the lateral, rather than medial, surface of the distal half of the anterior process. Two elements found with the holotype of *Euhelopus*, but not described by Wiman (1929), undoubtedly represent the quadratojugals. They differ from that in *Camarasaurus* in having a relatively longer anterior process that does not expand distally as quickly or as greatly. In *Diplodocus*, *Nemegtosaurus*, and the very similar *Quaesitosaurus*, the dorsal process is shorter and inclined slightly posteriorly. In *Plateosaurus* the quadratojugal differs from that in *Camarasaurus* in that the anterior process is shorter and more slender, and the dorsal process is inclined anteriorly about 30° from the horizontal.

Quadrate.—Well-preserved examples of the quadrate are plentiful. In addition to the quadrates of the articulated skulls AMNH 467, YPM 1905, CM 11338, and USNM 13786, there are the disarticulated examples DNM 28, AMNH 5761, and UVP 1984 (l), 2625 (l), 3683a (l), 5643 (r) (mate of 2625), 5679 (l), and 10795 (r). Finally,

the quadrates DNM 1009 and DNM 975 (l), which are still in place in the quarry, have the medial and posterior surfaces exposed, respectively.

The shaft of the quadrate is positioned nearly vertically to the ventral rim of the skull, but is bowed slightly anteriorly. A sinuous sutural scar extends along the entire lateral surface of the shaft for the squamosal and quadratojugal, and its rugose texture becomes more accentuated ventrally. The upper half of the scar received the squamosal, which nearly envelops the lateral surface of the blunt, slightly backwardly inclined head of the quadrate, whereas the lower half marks the articulation with the quadratojugal. In posterior view the shaft is straight, but approximately the distal fourth is greatly expanded laterally. A deep, trough-like depression occupies the upper two-thirds of the posterior surface of the shaft. Bounding the depression medially is a stout, smoothly rounded ridge that extends from the proximal head to the distal articular surface. A lower laterally bounding ridge forms the posterior margin of the anteriorly directed, mediolaterally thin, vertical pterygoid process, which is triangular in lateral and medial views. There is a shallow concavity on the lateral surface near the shaft and a broad, more distinct depression near the central area of the medial surface. A large sutural scar for the quadrate process of the pterygoid extends along the ventral border of the medial surface of the pterygoid process. The pronounced expansion of the very distal end of the shaft into a massive, foot-like base accommodates both a posterolaterally and a ventrally facing articular surface. In ventral view the entire articular surface is anteroposteriorly suboval in outline and is divided into a convex medial and a concave lateral portion.

The quadrate is among the most conservative elements of the sauropod skull and that in *Plateosaurus* is also distinctly like that in sauropods except the distal articular foot has a grooved surface ventrally, lacks a trough-like depression on the posterior surface of the shaft, and the pterygoid process does not extend quite as far forward. The quadrate in *Brachiosaurus* very closely resembles that in *Camarasaurus* except the head of the shaft is larger and inclined more posteriorly. There are no significant differences between the quadrates in *Euhelopus* and *Camarasaurus*. Those in *Diplodo-*

cus and *Apatosaurus*, and apparently *Nemegtosaurus* and *Quaesitosaurus*, are very similar to that in *Camarasaurus* except that they are much more slender, the depression on the posterior surface of the shaft is very shallow, the pterygoid process is positioned slightly lower on the shaft, and the entire dorsal half of the shaft is arched posteriorly. In *Antarctosaurus*, however, the proximal head is little inclined posteriorly, and the posterior surface of the shaft is slightly sculptured.

Squamosal.—The squamosals are present in the skulls YPM 1905, CM 11338, and CM 13786, where their lateral and dorsal aspects are well displayed (Fig. 1A, C, D; 6C; 21). In DNM 28 both squamosals are firmly sutured with the postorbitals and, except for being somewhat incomplete at their distal ends, are otherwise well preserved. The right squamosal of YPM 1912 is articulated with the postorbital and parietal. Squamosals among the Cleveland-Lloyd material include UUVP 3507 (l), 5806 (l), 10795 (l), 4020 (r, may be mate to 3507), and 10064 (p). All are nearly complete except for UUVP 4020 which lacks the ventral end. In DNM 975 and 1009 the complete right squamosals are exposed in lateral view and exhibit the distal end quite clearly, as the quadratojugals are disarticulated (Fig. 6C).

In lateral view the squamosal has the general shape of a question mark. The hooked dorsal head has a deep V-shaped notch on its lateral surface into which inserted the posterior process of the postorbital. From the posterior termination of the postorbital notch a pronounced ridge extends posteroventrally along the upper portion of the posterior margin of the descending shaft. A sharply defined concavity on the posteromedial face of the descending shaft encompasses most of the anterior and lateral surfaces of the dorsal half of the quadrate. The more deeply pocketed upper end of the cavity receives the head of the quadrate. The anterior surface of the descending shaft forms the dorsal portion of the posterior wall of the infratemporal fenestra, whereas dorsally it continues as the ventral surface of the hook-like anterior projection of the dorsal head of the squamosal to form the dorsal corner of the fenestra. The slightly tapered ventral end of the descending shaft overlaps laterally the dorsal process of the quadratojugal. The medial face of

the dorsal head of the squamosal forms the ventrolateral rim of the supratemporal fenestra, uniting anteriorly with the postorbital and posteriorly with the parietal. Just above the postorbital notch the dorsal surface of the head is transversely expanded into a broad, shelf-like structure whose rugose, irregular face narrows as it slopes steeply posteroventrally from its contribution to the posterior rim of the supratemporal fenestra. It is essentially this portion of the squamosal that is exposed on the occiput. At the dorsomedial margin of the shelf is a rugose sutural scar for the distal end of the wing-like, posterolateral process of the parietal. A smooth, shallow, concave depression along the ventral portion of the medial margin of the shelf receives in an abutment contact the approximately upper half of the anterior margin of the distal end of the paroccipital process of the braincase.

The squamosals in *Brachiosaurus* and especially *Euhelopus* are almost indistinguishable from that in *Camarasaurus*. Although Wiman (1929) correctly identified the squamosal and its V-shaped postorbital notch in *Euhelopus*, he mis-interpreted its orientation so that the left squamosal of his skull reconstruction is positioned upside down. In *Diplodocus* the postorbital notch is wider and the descending shaft does not contact the dorsal process of the quadratojugal. This also appears to be true in *Dicraeosaurus*, where the bone is more reduced. In *Nemegtosaurus* the descending shaft does not reach the quadratojugal, the body is unexpanded so that the entire element appears straight, and the postorbital joins the squamosal along a parallel-sided, rather than a V-shaped, slot. The squamosal in *Antarctosaurus* appears to be like that of *Diplodocus*. The squamosal in *Plateosaurus* is different in that the entire element is more slender, the postorbital articulation is longer, and the descending shaft is very slender and does not cup the head of the quadrate.

BRAINCASE

The massive braincase and lower jaws are the most commonly preserved parts of the *Camarasaurus* skull. As in all sauropods, the braincase is completely ossified, but in most of the articulated skulls only the dorsal and occipital aspects of the braincase are available for study. Generally the

lateral and ventral aspects have not been exposed (USNM 13786, DNM 975), or only partly exposed (CM 11338), or crude plaster restoration obscures sutures (AMNH 467). The latter case is true of YPM 1905, but under Marsh's direction most of the individual elements had been completely worked out, largely disarticulated, and illustrated in several views (Fig. 27, 28, 31, 32) before being reassembled. Several well-preserved and well-prepared braincases disassociated from other skull elements and available for study include DNM 28 (described by White, 1958); UUVP 3568, 10795, and 10070; AMNH 673 and 6126; BYU 9048; and CM 11969 (Fig. 22–26). AMNH 5761 (Fig. 4D, E), although not as complete as other specimens, has been sectioned along the midsagittal plane (Osborn and Mook, 1921), providing invaluable information about the endocranial cavity. Much of the right side of the braincase of DNM 1009 has been prepared. The essentially complete braincases CM 11969 and YPM 619 have been only roughly prepared at this writing. Finally, the incomplete braincase of YPM 1907 was skillfully disarticulated and prepared to expose contact surfaces of several elements not seen in any other specimen (Fig. 30, 33). This is particularly important because many of the elements in the adult sauropod braincase become fused and the sutures become indistinct. Additional isolated or partially isolated examples of most of the braincase elements are available for study (Fig. 27–33).

Brief descriptions of the braincase of *Camarasaurus* have been given by Marsh (1896), Huene (1914), and Osborn and Mook (1921), whereas White (1958) described the braincase of DNM 28 in detail. DNM 28 was prepared with great care and provides the best example of some of the very fragile laminae of the lateral surface of the braincase. Partly because of the remarkable preservation of this skull, there was some reluctance to risk too extensive preparation, and as a result White (1958) was unable to discern many of the cranial sutures. In the description below, suturally discrete elements of the braincase of *Camarasaurus* will be treated separately, but, because braincases of sauropods are rarely represented by disarticulated elements, the general comparisons of the braincases will follow after all the individual bones have been described.

Supraoccipital.—The supraoccipital is well-preserved in numerous crania (see Appendix 1), but only in YPM 1905 and UUVP 3568 (Fig. 23D, 27) are its sutures with neighboring elements discernible. The supraoccipital in DNM 28, encased in plaster at the time of White's (1958) description of the cranium, is now exposed (Fig. 23A). In addition, the preserved left half of the supraoccipital in YPM 1907 (Fig. 30A, B), which is firmly sutured with the exoccipital–opisthotic complex, also provides useful information.

The supraoccipital is one of the most massive elements of the cranium. In occipital view it is subtriangular in outline. The dorsal apex is variably developed in the Cleveland-Lloyd specimens. The occipital surface of the supraoccipital slopes anterodorsally, and a prominent crest is present in most specimens at its dorsal apex. The dorsolateral sides of the supraoccipital abut against the ventral margins of the lateral, wing-like processes of the paired parietals, whereas ventrally it unites with the paired exoccipital–opisthotic complexes (see below) except where it forms the dorsal margin of the foramen magnum.

In anteroventral view the disarticulated supraoccipital in YPM 1905 shows two adjoining pairs of elongate, rectangular, ribbed sutural surfaces that are separated by a deep, narrow channel that is the posterior wall of the endocranial cavity. The posterior pair of articular surfaces face ventrolaterally and contacted the exoccipital–opisthotic complex, whereas the anterior pair face anteroventrally and slightly laterally and are for the prootics. The incomplete supraoccipital in YPM 1907 shows the complete articular surface for the left prootic (Fig. 30D, E), and, though the left exoccipital–opisthotic complex is firmly joined to it, the suture between them is clear. Although the occipital surface of the supraoccipital slopes anterodorsally, the posterior wall of the endocranial cavity slopes only very slightly in this direction due to progressive anteroposterior thickening ventrally of the bone in this region.

Exoccipital–opisthotic.—The exoccipital and opisthotic are never found disarticulated, nor have they ever been manually separated, and for this reason the two elements will be described as a unit. Although the grain of the bone leaves little doubt as to the position of the suture between the

exoccipital and opisthotic, in no specimen examined by us, including the most juvenile, can a definite suture be discerned. This indicates fusion at an early stage of growth. In addition to the articulated crania noted in Appendix 1, the following disarticulated materials from Como Bluff afford the best detailed information of this complex: multiple-view drawings of the articulated prootic and exoccipital–opisthotic complex in YPM 1905 prepared for Marsh (Fig. 28), and the isolated right and left exoccipital–opisthotic complexes in YPM 1907 and 1912 (Fig. 29, 30A–G).

The approximate position of the union between the exoccipital and opisthotic on the occiput is indicated in Fig. 29B. Extending ventrally from the body of the exoccipital–opisthotic complex is a foot-like structure composed almost entirely of the exoccipital. It forms the extreme posteroventral corner of the lateral wall of the braincase and encloses two closely set canals for cranial nerve XII, the smaller, more posterior of which carried a branch. The two canals emerge in a groove on the lateral surface of the braincase just posterior to a low ridge that delineates the juncture of the exoccipital and opisthotic. The flat, anteroposteriorly elongated ventral surface of the foot-like base of the exoccipital unites with the basioccipital. Approximately the posterior third of this structure extends beyond the occipital plane, where it contributes minimally to the dorsolateral margin of the occipital condyle and articular surface. The dorsolateral margin of the foramen magnum is formed by a short, blunt extension of the exoccipital which overlaps the occipital surface of the supraoccipital and nearly meets that of the opposite side, thereby almost excluding the supraoccipital from the foramen rim. At the level of the foramen magnum the exoccipital extends laterally as a narrow, wing-like extension over the occipital surface of the opisthotic to within one-fourth of the distance to the distal end of the paroccipital process.

The opisthotic is a large, block-like element that comprises the greater part of the paroccipital process and is bounded posteriorly by the exoccipital and anteriorly by the prootic. At the level of the upper end of the small posttemporal fossa the paroccipital angles downward. Here it constricts in breadth slightly along its dorsal

margin as it bounds the medial margin of the posttemporal fossa, then expands again distally, where it contacts the squamosal and quadrate. Above the endocranial cavity the medial face of the opisthotic has a ventromedially elongate, ribbed, subrectangular sutural surface for the supraoccipital. The sutural scar on the opisthotic for the prootic is extensive and divisible into two adjoining areas. The larger of the two areas covers nearly the proximal third of the anterior face of the paroccipital process and appears as a broad area of laterally radiating striations. Along its medial edge is a narrow, ribbed strip that makes a broadly obtuse angle with the radially striated area and an abrupt angle of 80° with the articular surface for the supraoccipital. A short distance anterior to the foramina for cranial nerve XII and near the original opisthotic–exoccipital boundary is a large circular opening often referred to as the jugular foramen that presumably transmitted cranial nerves IX–XI and probably the jugular vein.

Prootic.—The prootic is exposed in lateral view in the braincases of DNM 28; UUVP 3568, 10795, and 10070; CM 11969; and AMNH 973, 5761, and 6126 (Fig. 22–26). It is one of the most difficult elements of the skull to study and figure for several reasons: an unusually large part of it is covered by neighboring elements, the sutures with adjoining elements are difficult to determine in mature specimens, and the very fragile crista prootica is angled so strongly posteriorly as to make openings in the lateral wall posterior to it difficult to see. For this reason the success of Marsh's technicians in disarticulating the prootic has been very helpful, even though that in YPM 1905 and to a greater degree YPM 1907 and 1912 (Fig. 29, 30C–E) is incomplete, particularly the lower portion of the crista prootica. The crista prootica is well preserved in the prootics of DNM 28 and UUVP 10795, and the ventral portion and nerve openings are clearly seen in AMNH 5761 and UUVP 3568.

The prootic is an extensive element bounded by the opisthotic and supraoccipital posteriorly, the basioccipital and basisphenoid ventrally, the laterosphenoid anteriorly, and the parietal dorsally. It is tightly sutured to all of these elements except the laterosphenoid and parietal, with which it has

abutment contacts. The upper, main portion of the prootic is block-like. The articular surfaces for the opisthotic and supraoccipital are clearly visible on its posterior surface. A broad, striated sutural scar for the opisthotic occupies the lower portion of the posterior surface, and its dorsal margin is delineated by a straight, narrow groove. Above the groove and sloping anterodorsally at an angle of about 45° to the sutural surface for the opisthotic is a large, rough articular surface for the supraoccipital. The smooth, rounded dorsal crest abuts the ventromedial edge of the posterolateral wing of the parietal. Medially the main body of the bone forms part of the lateral wall of the endocranial cavity.

The prootic is exposed on the external surface of the braincase mainly as a smooth, slightly concave, expansive surface that extends posterolaterally onto the anterior surface of the proximal portion of the paroccipital process of the opisthotic and, thus, faces anterolaterally. Beneath the level of its contribution to the paroccipital process the prootic forms a thin, laterally projecting lamina of bone, the crista prootica. It extends ventrally below the level of the floor of the endocranial cavity, where it continues for a considerable distance along the lateral surface of the basisphenoid, terminating at the base of the basiptyergoid process. In anterior view the lateral edge of the crista prootica is smoothly concave, and the distal portion, which broadens slightly, has a very rugose surface. The lower portion of the prootic forming the lateral wall of the endocranial cavity encloses one foramen and borders two others. On the prootic–opisthotic suture just above the basioccipital the prootic forms the anterior border of the fenestra ovalis (VIII). Directly anterior to the fenestra ovalis is a small foramen for the facial nerve (VII) that opens onto the posterior face of the crista prootica. At the same level as the foramen for the facial nerve and on the prootic–laterosphenoid boundary is a large, subcircular opening for the trigeminal nerve (V).

Laterosphenoid–orbitosphenoid.—Forming the lateral wall of the braincase anterior to the prootic and dorsal to the basisphenoid is the laterosphenoid. The presence of a separate element, or elements, anterior to the laterosphenoid and referred to as the orbitosphenoid and/or presphe-

noid has been reported often in dinosaurs, but rarely is a distinct suture observed. Madsen (1976) described a laterosphenoid–orbitosphenoid suture in the theropod *Allosaurus*. Although Janensch (1935–1936) recognized both the laterosphenoid and orbitosphenoid in *Brachiosaurus*, *Barosaurus*, and *Dicraeosaurus*, and Osborn (1912:fig. 12, 16) recognized an orbitosphenoid (=laterosphenoid) and presphenoid in *Diplodocus*, neither author described a suture separating them. Similarly, in YPM 1907, which otherwise clearly exhibits most of the braincase sutures, a laterosphenoid–orbitosphenoid suture (Fig. 31) cannot be found. Most recently, however, Berman and McIntosh (1978) described a distinct suture separating the laterosphenoid and orbitosphenoid in a *Diplodocus* braincase (CM 26552). They also noted the possible presence of fragments of a thin, vertical plate of bone oriented on the midsagittal plane just anterior to the orbitosphenoid in *Diplodocus* (CM 11161) that may represent remnants of the presphenoid. Of the *Camarasaurus* specimens examined by us, a laterosphenoid–orbitosphenoid suture has been definitely detected only in the articulated braincases UVP 3568 and 10795 (Fig. 22–26). In these specimens the suture has the same position and divides identical areas of the braincase as described by Berman and McIntosh (1978) in *Diplodocus*. There can be little doubt that both the laterosphenoid and orbitosphenoid are present in *Camarasaurus*, but the separating suture may not be traceable in most specimens likely due to fusion at an early stage of growth. Although there is little doubt as to the position of the suture, the two elements are here described together as a complex. Early descriptions often refer to the laterosphenoid as the “alisphenoid,” but we follow Janensch (1935–1936) and most modern authors in the use of laterosphenoid. As Romer (1956) pointed out, the laterosphenoid is not the homologue of the mammalian alisphenoid and, therefore, the latter name is not appropriate in the description of reptilian osteology. The only instance of an isolated laterosphenoid–orbitosphenoid complex of *Camarasaurus* is an imperfect example in YPM 1907 (Fig. 31). The complex is therefore described here essentially as it is exposed in lateral view of the braincase (Fig. 22–26).

The laterosphenoid portion of the complex is a narrow, wing-like structure that is exposed mainly as a flat, anteriorly facing surface. A short distance above its narrow, digitating suture with the basisphenoid the laterosphenoid bounds the anterior margin of the trigeminal foramen. On the basis of the braincases UUVP 3568 and 10795 referable to *Camarasaurus*, and the description of the braincase of *Diplodocus* by Berman and McIntosh (1978), the laterosphenoid-orbitosphenoid suture can be confidently described as extending directly dorsally from the basisphenoid contact, passing first through the foramen for the oculomotor nerve (III) a very short distance above the basisphenoid and then through the foramen for the trochlear nerve (IV) a short distance below the dorsal extent of the complex. Above the level of the trigeminal foramen the laterosphenoid expands outward as it extends upward, forming a thick laterally arching, wing-like lamina of bone, the crista antotica. The dorsal margin of the crista contacts the ventromedial edge of that portion of the postorbital forming the anterior wall of the supratemporal fenestra. This contact is almost completely hidden in anterior view of the braincase by the posterolateral wing of the frontal that overlaps the anterior surface of the postorbital to form the medial half of the posterior wall of the orbit.

The stout, broadly convex orbitosphenoid portion of the complex, which forms the anteriormost component of the lateral wall of the braincase, converges with its mate anteriorly on the midline so as to face anterolaterally. Because the orbitosphenoids gradually expand anterodorsally, their midline union is inclined anterodorsally, so that they form an anterodorsally sloping floor of the endocranial cavity anterior to the basisphenoid. The orbitosphenoid has strong, interdigitating sutures with the frontal dorsally and the fused basisphenoid-parasphenoid ventrally. A large, circular, anterolaterally directed opening for the optic nerve (II) pierces the orbitosphenoid a short distance anterior to the trochlear foramen and close to its anterior midsagittal union with its mate. That portion of the orbitosphenoid posterior to the optic foramen and forming the anterior margins of the oculomotor and trochlear foramina has the form of a stout, vertical pillar. A short,

thick process projects posteriorly from the pillar-like posterior margin to separate the oculomotor and trochlear foramina. The orbitosphenoids form a large V-shaped notch at the dorsal extent of their anterior midsagittal union for the passage of the olfactory nerve (I); the frontals roof the olfactory foramen.

Basioccipital.—The basioccipital is present in all of the reported crania (see Appendix 1). Description of its endocranial aspects, however, relies heavily on the articulated basioccipital and basisphenoid-parasphenoid complex in YPM 1901 and 1905 (Fig. 32A–G), and the articulated basioccipital and basisphenoid in UUVP 5684 (Fig. 32H–J).

The basioccipital forms all but the very small dorsolateral portions of the neck and articular surface of the large occipital condyle contributed by the exoccipitals. The articular surface is hemispherical except for being slightly flattened dorsally. The long axis of the condyle is directed posteroventrally at an angle of about 45° to a plane passing through the alveolar margins of the jaw. The dorsal surface of the basioccipital exhibits a narrow, shallow trough that begins posteriorly at the level of the foramen magnum and continues anteriorly along the floor of the braincase to the anterior margin of the bone. The trough, which is nearly uniform in width and depth, is flanked by ribbed sutural surfaces that are wider than the trough and slope ventrolaterally at about 45° to the horizontal. For most of their posterior length the sutural surfaces received the exoccipitals, whereas anteriorly they received the opisthotics and prootics. From the anteroventral margin of the articular surface of the condyle the inferior surface of the basioccipital arches anterodorsally, then curves smoothly ventrally and slightly posteriorly to form the greater posterior portions of the robust and relatively short basal tubera. The tubera diverge ventrolaterally from one another at an angle of about 45°, with a small but deep subspheroidal depression separating them.

Basisphenoid-parasphenoid.—The basisphenoid forms the cranial floor anterior to the basioccipital. It is completely fused with the parasphenoid, which is represented by the parasphenoidal rostrum. In no sauropod, or to our knowledge any saurischian, is there any evidence of a suture

between the basisphenoid and parasphenoid; this is true of even the most immature individuals. It is, therefore, impossible to determine how much, if any, of the anterior surface of the basisphenoid, including the basiptyergoid processes, may have been covered by the parasphenoid. The basisphenoid is present in most of the reported crania (Fig. 22–26) (see Appendix 1). Of the partially disarticulated examples of the basisphenoid, the endocranial aspects are best exhibited in YPM 1901 and 1905, and DNM 28 (Fig. 22A; 32B, I). Complete, or nearly complete, parasphenoids occur in the braincases of CM 11969, DNM 28, UUVP 4286, 10070, and 10975, and YPM 1905 and 1907 (Fig. 22–26, 32, 33A).

The basisphenoid forms a small, anterior portion of the basal tubera and at least the greater portion of the long, stout basiptyergoid processes, which typically diverge ventrolaterally at approximately a 45° angle from one another. A strong ridge runs the length of the anterior margin of each process which terminates distally as a rough, rounded end. A broad, smooth, slightly concave triangular surface occupies the area between the bases of the basiptyergoid processes and the parasphenoidal rostrum. The narrow, smooth channel of the endocranial floor on the dorsal surface of the basioccipital continues a short distance anteriorly onto the dorsal surface of the basioccipital. It terminates at the transverse ridge of the dorsum sellae which forms the posterior border of the large circular opening of the sella turcica or pituitary fossa. On either side of the smooth endocranial floor on the dorsal surface of the basisphenoid is an irregular, rugose sutural scar for the laterosphenoid that rises anteriorly somewhat above the level of that on the dorsal surface of the basioccipital. The vertically elongate pituitary fossa extends ventrally to a level just below the base of the parasphenoidal rostrum. The upper half of the cavity gradually enlarges slightly, then constricts slightly before enlarging significantly into a distal, subspherical chamber (Fig. 34). Small, paired foramina pierce the posterior wall, or dorsum sellae, of the pituitary fossa for the passage of the abducens nerve (VI). Each nerve, presumably along with the palatine branches of the carotid artery and facial nerve, exits the endocranial cavity via a canal that extends from

near the floor of the pituitary fossa to a small round opening on the lateral surface of the basisphenoid directly below the foramina for cranial nerves III and IV.

In lateral view the parasphenoidal rostrum is narrowly triangular, with the apex directed anteriorly. Its straight dorsal margin occupies a level that is parallel to and just below that of the floor of the endocranial cavity. In cross section the rostrum is a thin, blade-like structure, but with the inferior margin expanding slightly proximally as it joins the body of the braincase.

Scleral Ossicles.—In the right orbit of CM 11338 as reported by Gilmore (1925:plate X) are several clearly visible fragments of bone representing a ring of scleral ossicles. As Gilmore observed, the state of preservation is too poor to permit a determination of the number, shape, or arrangement of the individual plates. A second, somewhat better preserved ring of scleral ossicles is present in the left orbit of an undescribed skull (USNM 13786; Fig. 1D). Unfortunately, preservation does not reveal details of its structure, other than having an overall form of a circular band of bone which slopes medially away from an axis central to the ring. The presence of a ring of scleral ossicles in *Camarasaurus* is not unexpected, inasmuch as it has been reported in *Diplodocus* (Holland, 1924) and *Nemegtosaurus* (Nowinski, 1971).

Stapes.—The stapes has not been described in any sauropod, although it has been recognized in several other saurischians, such as *Plateosaurus* (Huene, 1926), *Dromaeosaurus* (Colbert and Ostrom, 1958), and *Allosaurus* (Madsen, 1976). Most importantly, well-preserved stapes in what are presumably their near-proper positions are present in the skull of CM 11338 (Fig. 5E).

On the basis of CM 11338 the stapes is a slender, nearly straight rod that is subcircular in cross section and gradually increases in diameter distally. Except for their proximal few millimeters, the entire length of both stapes in CM 11338 have been exposed in posterior view. The exposed length of both elements is about 25 mm, and their total length is probably about 30 mm. Both stapes occupy identical positions with respect to the braincase, presumably articulate within the fenestra ovalis, and project in identical ventrolateral angles.

Due to distortion of the skull roof, however, their distal ends exhibit different relationships with the quadrate. The distal end of the right stapes lies about 2 mm anterior to the anterodorsal margin of the proximal portion of the pterygoid process at a level of about 1.5 cm below the dorsal end of the shaft, whereas the distal end of the left stapes contacts the medial surface of the pterygoid process at the same horizontal level and about 1.5 cm from the posterior margin of the quadrate. The left stapes presumably retains the more correct relationship with the quadrate.

Comparisons.—Cursory comparisons of the various sauropod braincases reveals that they are for the most part fundamentally similar. Several differences do stand out, the most obvious being the length and robustness of the basiptyergoid processes and basal tubera. The size of the occipital condyles also varies noticeably, but this apparent variation could be more a function of maturity than taxonomic diversity.

Of the three genera having skulls most similar to *Camarasaurus*, the braincase is unknown in *Euhelopus* (Wiman, 1929) and known by only two elements in *Pleurocoelus* (Lull, 1911), whereas it is completely known in *Brachiosaurus* (Janensch, 1935–1936). In the last-mentioned genus the basiptyergoid processes are somewhat longer and more slender, the basal tubera are much less prominent, the parasphenoid is less expanded vertically, and the openings for cranial nerve II are smaller and closer together. In *Pleurocoelus* only the supraoccipital and slightly imperfect laterosphenoid are preserved. The supraoccipital resembles that in *Camarasaurus*, but the channel forming the posterior wall of the endocranial cavity maintains a uniform width throughout its length, and the sutural contact with the parietal is much reduced. The dorsal crest of the occipital surface is much less pronounced, but this may be a juvenile feature. The laterosphenoid in *Pleurocoelus* is also similar to that in *Camarasaurus*, minor differences being that in the former the opening for cranial nerve II is larger, whereas those for cranial nerves III and IV are somewhat smaller.

The braincases of *Diplodocus*, *Dicraeosaurus*, *Nemegtosaurus*, *Quaesitosaurus*, and *Apatosaurus* differ from that of *Camarasaurus* in that the

basiptyergoid processes of the former genera are much longer, more slender and cylindrical, and directed anterolaterally rather than ventrolaterally, the basal tubera diverge only slightly ventrolaterally, and the paroccipital processes are longer and narrower in vertical width. In *Antarctosaurus* the basiptyergoid processes, although incompletely known, are more slender and longer than those in *Camarasaurus*. Nowhere are differences more evident between the sauropods and prosauropods, as exemplified by *Plateosaurus*, than in the braincase. Most notably, in the braincase of *Plateosaurus* the anterior end is completely open, the laterosphenoid is greatly reduced, particularly the lateral extent of the crista antotica, the paroccipital process is much longer and directed not only ventrolaterally but also posteriorly, the parasphenoid is very elongate, having a length equal to those of the basisphenoid and basioccipital combined, and the anterior wall of the pituitary fossa remains unossified.

PALATE

Many of the major questions regarding the cranial anatomy of *Camarasaurus* can now be resolved with the recent preparation of the palate in CM 11338 (Fig. 35). However, preparation was limited to the oral or ventromedial surface, and questions concerning the aboral or dorsolateral surface of the palate could only be answered with disarticulated elements. It is likely that the skull USNM 13786 also possesses an articulated palate, but it probably will not be prepared in the foreseeable future. It was hoped that one or both of the two excellently preserved skulls on the quarry face at Dinosaur National Monument might possess an articulated palate. Unfortunately, further preparation of DNM 975 has revealed only four preserved palatal elements, and they are somewhat displaced. The pterygoids, left ectopterygoid, and right palatine were discovered closely associated with the skull, and the right pterygoid and palatine were subsequently removed from the quarry and prepared. Similarly, some of the palatal elements of DNM 1009 are absent and perhaps missing. The pterygoid is the only palatal bone to have been correctly identified and described (White, 1958). White (1958), however, also figured a prearticular

incorrectly as a vomer and an ectopterygoid as an unidentified element.

Openings.—Four paired and one single opening of the palate can be identified and listed in order of their decreasing size: subtemporal fenestrae, choanae, interpterygoid vacuity, subnarial foramina, and postpalatine foramen. The palate of *Camarasaurus* is so highly vaulted that the planes of the lateral halves occupy a more vertical than horizontal position. Consequently, the outlines of the various palatal openings are distorted to appear narrower in directly ventral or medial views.

The anteroposteriorly elongate, oval subtemporal fenestra is bounded by the quadratojugal and jugal laterally, the maxilla and ectopterygoid anteriorly, the pterygoid medially, and the quadrate posteriorly. The large choanae are also anteroposteriorly elongate and oval, but relatively a little broader. They are bounded by the maxillae laterally, the vomers medially, and the palatines posteriorly. The interpterygoid vacuity is roughly circular, with the pterygoids bounding its anterior and the basipterygoid processes its posterior half. The parasphenoidal rostrum partially divides the opening posteriorly. The subnarial foramina are very small and bounded laterally and posteriorly by the medial process of the maxilla and medially and anteriorly by the posteriorly projecting, ventral, or internal, component of the dorsal maxillary process of the premaxilla. Lastly, the extremely small postpalatine foramina are bordered in almost equal proportions by the palatal shelf of the maxilla, the maxillary process of the palatine, and the ectopterygoid.

Pterygoid.—A major portion of the pterygoid is preserved in the paratype of *Camarasaurus grandis* (YPM 1905, Fig. 36A–D), described by Marsh (1879), and in *Camarasaurus supremus* (AMNH 5761, Fig. 4C), described by Osborn and Mook (1921). Paired elements are preserved and exposed in ventral aspect in AMNH 467. The ventromedial surfaces of the paired pterygoids in CM 11338 have been exposed, which are complete and excellently preserved except for slight displacement. Preparation of the two disarticulated and virtually complete pterygoids in the skull DNM 28 (Fig. 36J–M) allowed White (1958) to present the first description with drawings of this element. The Cleveland-Lloyd quarry has yielded

four nearly complete pterygoids (Fig. 36E–I, Q–Y), three right (UUVP 1986, 3369, 10795), one left (UUVP 3350), and several fragmentary left pterygoids (UUVP 4309, 5259). Finally, the ventromedial surface of the left pterygoid of DNM 975 has been exposed in detail on the quarry face at Dinosaur National Monument, whereas the displaced right has been removed and prepared. Similarly, the ventromedial surface of the left pterygoid in DNM 1009 has been prepared in place.

The pterygoid is by far the largest of the four paired elements of the sauropod palate. It is an irregularly-shaped plate that stands at about 60° to the horizontal, and with its mate forms most of the highly vaulted palatal surface. It is a triradiate bone with an anterior process, a lateral transverse process, and a posterior quadrate process. The anterior process has the form of a broad, wing-like plate that tapers anteriorly to a point. The paired pterygoids narrowly contact one another along the dorsal border of the ventromedial surface of their anterior processes in a straight medial suture. The dorsolateral surface of the narrow pointed end of the anterior process is overlapped by the vomer. Also on the dorsolateral surface is a distinct palatine ridge which extends obliquely antero-dorsally from near the juncture of the anterior and lateral transverse processes that marks the line of contact with the posterior edge of the palatine. The slender transverse process is directed abruptly downward and slightly backward at its midlength, then tapers to a blunt point which nearly reaches the level of the lower margin of the maxilla. A vertical notch along the anteromedial margin of the transverse process receives the lateral edge of the expanded, plate-like medial process of the ectopterygoid. The posteriorly directed quadrate process tapers distally. Its lateral surface is sutured firmly to the medial surface of the large pterygoid process of the quadrate in a wide, usually rugose contact. In the middle of the dorsal surface of the process is a deep circular depression, the basipterygoid pit, into which the basipterygoid process of the basisphenoid inserts. A blunt, tooth-like projection is directed laterally from the postero-medial margin of the basipterygoid pit. In his original, brief description of the skull of *Morosaurus grandis* (YPM 1905), Marsh (1879) inexplicitly

cably misinterpreted the lateral and medial faces of a disarticulated portion of the skull containing the quadrate, pterygoid, and quadratojugal. This resulted in a misidentification of the pterygoid as the quadratojugal and vice versa. Figures of the back of the skull were prepared in multiple views, one of which was published by Marsh (1880:254) as erroneously showing the dorsal pit for the basiptyergoid process on the lateral surface of the skull. Marsh detected the error several years later, however, and amended figures were published (Marsh, 1896:plate XXX; Fig. 2).

Only very minor differences distinguish the pterygoids in *Camarasaurus* and *Brachiosaurus*. In the latter the anterior process is slightly longer, and the quadrate process is slightly broader vertically, expanding its area of articulation with the quadrate. As figured by Wiman (1929), the pterygoid in *Euhelopus* differs considerably from those in *Camarasaurus* and *Brachiosaurus*, most particularly in the enormous expansion of the anterior process, which extends to essentially the anterior border of the palate. As shown by Wiman, at a level very nearly equal to the distal end of the nasal process of the maxilla the anterior process of the pterygoid unites with the distal end of the lacrimal. Such a marked departure in organization from that of all other sauropod skulls is quite unlikely. Part of the misinterpretation is clearly a result of incorrect positioning of the quadrate and the 180° rotation of the squamosal, as discussed above. If the quadrate is rotated into a more vertical position, as in *Camarasaurus*, and positioned more dorsally within the skull, then the anterior end of the pterygoid assumes a more typical sauropod position near the level of the ventral margin of the naris. Yet, the shape of the pterygoid in *Euhelopus* is very different from that in other forms, assuming Wiman (1929:plate II, fig. 5, 6) is correct. The quadrate process is reduced, with the articular surface for the quadrate being even smaller yet than in *Camarasaurus*. The length of the transverse process is also reduced and, rather than being vertically oriented, is angled strongly medially. The anterior process, as he illustrated it, is greatly elongated, broadened, and, most importantly, directed strongly anterodorsally. Major differences also exist between the pterygoids in *Camarasaurus* and *Diplodocus*. In the

latter the anterior process is not only much longer, but the position of its upper border, along which it articulates with its mate, is also considerably longer. Additionally, the transverse process is shorter and thinner in transverse section. In *Plateosaurus* the wing-like anterior process is longer, the transverse process is very much like that in *Diplodocus*, and the quadrate process is broader vertically and thinner mediolaterally, with no basiptyergoid pit.

Ectopterygoid.—The ectopterygoid (Fig. 37), or transverse bone of some authors, has not previously been reported in *Camarasaurus*, although one of a well-preserved pair belonging to DNM 28 was illustrated and identified by White (1958) as an unknown element. Many years earlier an ectopterygoid belonging to YPM 1912 was correctly identified by Marsh and his coworkers, and, although he had it prepared and illustrated, a published description never followed; those drawings are presented here for the first time (Fig. 37A–E). A right ectopterygoid was found with AMNH 467, but was not incorporated into the mounted skull. The Cleveland-Lloyd collection includes three well-preserved ectopterygoids: UUVP 5115 (l), 4270 (l), and 5593 (r). The first is the largest, whereas the other two are the same size and may belong to the same individual. Partially exposed ectopterygoids are seen in the two skulls on the quarry face at Dinosaur National Monument, DNM 975 and 1009. The ventral aspect of the right and the ventral and dorsal aspects of the left ectopterygoid are exposed in the articulated palate of the skull of CM 11338.

The ectopterygoid is a small, rather simple element that consists, for the most part, of a narrow, lateral shaft and a vertically expanded, blade-like medial flange. The lateral shaft is oriented horizontally and angles posteromedially, as does the blade-like medial flange. The distal end of the lateral shaft is expanded ventrally into a small, flange-like lip that attaches firmly in a roughened depression at the extreme posterior end of the palatine shelf of the maxilla. At its midlength the lateral shaft is suboval in cross section, with a vertical height about twice the horizontal width. In anteromedial or posterolateral view the blade-like medial flange extends ventrally below the level of the lateral shaft as a long,

narrowly triangular projection which is slightly bowed posterolaterally. A roughened surface extending as a band across the dorsal margin of the anteromedially facing surface marks the area of contact with the palatine. The posteromedial surface fits into a step-like depression on the anteromedial surface of the transverse process of the pterygoid.

The ectopterygoid in *Brachiosaurus* is generally similar to that in *Camarasaurus*, but the lateral shaft is stouter and its distal end less expanded ventrally, and the area of articulation of the blade-like medial flange with the palatine is reduced. Differences from that in *Diplodocus* are more striking, where the distal end of the lateral shaft is greatly expanded anteroposteriorly into a thin horizontal plate that attaches to the ventral surface of the palatine shelf of the maxilla. Medially the ectopterygoid first contacts the ventral surface of the proximal end of the maxillary process of the palatine, then bends sharply ventrally and slightly anteriorly as a narrow, mediolaterally flattened blade which articulates with the anterior portion of the lateral surface of the distal end of the transverse process of the pterygoid. The ectopterygoid in *Plateosaurus* is similar to that in *Diplodocus*, but the lateral articulation is reduced, and the medial articulation with the pterygoid is expanded. Perhaps the greatest difference, as shown by Huene (1926), is that the lateral articulation is with the jugal rather than with the maxilla. In sauropods the jugal has become so reduced that the lateral articulation of the ectopterygoid has shifted forward from the jugal to the maxilla.

Palatine.—The only known examples of this element are those in the articulated palate of CM 11338 (Fig. 35), where only the oral surfaces have been exposed, and the completely exposed, isolated right palatine of DNM 975 (Fig. 38). Although it is likely that palatines are preserved in CM 13786 and perhaps in DNM 1009, preparation of these specimens has not proceeded far enough to confirm their presence.

The palatine is basically a narrowly subtriangular, thin plate which in the articulated palate is oriented nearly vertically with the oral surface facing medially and very slightly anteriorly. Extending anterolaterally from the anteroventral corner of the plate is a shaft-like maxillary process.

The maxillary process is roughly circular in cross section, and its distal end attaches firmly to an oval depression on the palatine shelf of the maxilla. The slightly thickened, smoothly rounded anterior edge of the plate, which forms the posterior margin of the choana, curves gradually anteriorly a short distance as it merges with the maxillary process. The slightly convex posterior edge of the plate unites with the pterygoid along the palatine ridge on its dorsolateral surface. The medial surface of the dorsal apex of the triangular plate articulates with the vomer. The ectopterygoid articulates loosely with the palatine along a narrow area extending across the ventral margin of the lateral surface of the palate and then continues onto the proximal portion of the maxillary process. The triangular plate is bowed slightly laterally, so that its oral surface is concave.

The palatine in *Diplodocus* occupies approximately the same position as that in *Camarasaurus*, and, although smaller, it is structurally similar. In sharp contrast the distal end of the maxillary process in *Diplodocus* has the form of a thin, horizontal, greatly expanded anteroposteriorly flange that contacts the ventral, rather than the medial surface of the palatine shelf of the maxilla. In addition, the vertical, plate-like structure bows medially in *Diplodocus*, so that the oral surface is convex. In *Brachiosaurus* the vertical plate of the palatine is narrowly subrectangular, but is also bowed laterally. The vertical plate of the palatine in *Euhelopus* (mistakenly referred to as the vomer by Wiman, 1929) is triangular, as in *Camarasaurus*, but is shorter and flat, whereas the maxillary process is similar except for being slightly less robust. Only the maxillary process of the palatine is known in *Nemegtosaurus*, and it most closely approximates that in *Diplodocus*.

Vomer.—The vomer ("prevomer" of Janensch, 1935–36) in *Camarasaurus* has heretofore never been described or illustrated. White (1958) erroneously described a left prearticular of DNM 28 as a vomer. The vomers in the articulated palate of CM 11338 (Fig. 35) have been partially exposed, the right more so than the left. A complete, isolated right vomer (Fig. 39), UUVP 5065, from the Cleveland-Lloyd quarry is the only other known example of this element.

The vomer is in general a mediolaterally flat-

tened plate having the outline of a broad-based isosceles triangle. The paired elements contact one another along the midline for about half of their anterior length, diverging slightly posteriorly. Following the orientation of the right vomer UUVF 5065 in Fig. 57, the ventral edge is greatly thickened and bluntly rounded and is the only portion of the element exposed on the aboral surface of the palate. The bluntly rounded anteroventral corners of the paired vomers are clasped together between the ends of the posteriorly directed ventral, or internal, components of the dorsal maxillary processes of the premaxillae. The medial surface of the vomer is essentially flat, whereas the lateral surface exhibits a considerable amount of relief. A small, beveled area on the margin of the lateral surface of the posterodorsal corner of the vomer marks the area of contact with the dorsal apex of the triangular, vertical plate of the palatine. A broadly convex swelling of the lateral surface parallels the ventral border of the vomer. This swelling is accentuated by a moderate excavation along almost the entire length of the lateral surface of the anterodorsal margin that gives it a knife-like edge. The anterior process of the pterygoid undoubtedly contacts the vomer along much of the dorsal portion of its medial surface. The absence of a distinct sutural scar on the vomer, however, prevents an accurate account of the contact.

Reports of sauropod vomers are rare. The vomer identified in *Euhelopus* by Wiman (1929) was shown by Janensch (1935–1936) to be the palatine. Nowinski (1971) reported an unpaired vomer with a peculiar transverse anterior process in *Nemegtosaurus*. McIntosh and Berman (1975) questioned this interpretation and believed that further preparation will reveal the vomer to be more nearly like that of other sauropods. An excellently preserved, medially exposed, disarticulated left vomer of the *Diplodocus* skull CM 3452 was described by McIntosh and Berman (1975). The same aspect of the left vomers is partially exposed in the articulated *Diplodocus* skulls CM 11161 and USNM 2672. The only other reported vomers are a pair belonging to the skull of *Brachiosaurus brancai* described by Janensch (1935–1936).

At first glance the vomers in *Camarasaurus*

and *Diplodocus* appear to be rather similar in that they are shaped like isosceles triangles with one angle broadly obtuse and the others acute. The vomer in *Diplodocus* is not only thinner and more elongate anteroposteriorly, but is oriented such that the broad base of its triangular form is ventral and the obtuse angle is directed dorsally. Surprisingly, the vomer in *Brachiosaurus* is not only unlike that in *Camarasaurus*, if properly restored by Janensch (1935–1936), but also that in *Diplodocus*. As restored by Janensch, the vomer is a mediolaterally thin, anteroposteriorly long plate having an outline of an inverted broad-based isosceles triangle with the obtuse angle directed ventrally. A sutural scar on the medial surfaces of the margins forming the ventrally directed obtuse angle was interpreted by Janensch as the area of contact with its mate. If, however, the vomer is rotated 180° through a sagittal axis so that the obtuse angle is directed dorsally, then it not only closely resembles that in *Diplodocus* in shape and orientation, but the articular scar identified by Janensch as for its mate now also duplicates in position and extent that identified for the anterior process of the pterygoid in *Diplodocus*.

MANDIBLE

The mandible, both rami of which are present in DNM 28 (Fig. 40A–D), CM 11338 (Fig. 5A, D; 41A–D), and DNM 975, is composed of eight elements, with the dentary, surangular, and angular exposed in lateral view and the articular, prearticular, splenial, coronoid, and intercoronoid exposed in medial view. The coronoid is described here for the first time in the Sauropoda. The jaw is relatively short and becomes increasingly thicker anteriorly. A strong dentition, consisting of 12 or 13 massive, spoon-shaped teeth, occupies all but the posteriormost portion of the dentary. There is no obvious external mandibular foramen in any of the articulated specimens. An elongate adductor fossa opens dorsally, with the medial lip occupying a slightly lower level than the lateral lip. The fossa is bounded posteriorly by the articular, medially by the prearticular, anteriorly by the coronoid, and laterally by the intercoronoid, dentary, and surangular. The angular floors the fossa, and, as in all saurischians, there is no

distinct coronoid process. In no known specimen of *Camarasaurus* has there been fusion of the mandibular symphysis.

The well-preserved and uncrushed rami of DNM 975 (Fig. 42) exhibit all sutures with remarkable clarity. Further, the articulated partial right ramus (Fig. 42D–G), which consists of the three lateral elements, has been removed from the Dinosaur National Monument quarry and completely prepared. This has allowed a detailed account of the morphology and interrelationships of the three elements in both lateral and medial aspects. The left ramus of DNM 975 (Fig. 37A–C) remains on the quarry face, but has been prepared in medial view and shows clearly the interrelationships of all the medial elements. The mandible in *Camarasaurus* resembles superficially those in *Brachiosaurus* and *Euhelopus* in that the symphyseal region is rounded in dorsal view and the dentition extends posteriorly to nearly its midlength, whereas in *Diplodocus*, *Nemegtosaurus*, and *Antarctosaurus* the dentition is restricted to the symphyseal region, which is rectangular in dorsal view. The broad, spatulate teeth in *Camarasaurus* are also much more similar to those in *Brachiosaurus* and *Euhelopus* than they are to the weak pencil-like teeth typical of diplodocids. The lower jaw of *Camarasaurus* differs from those in *Brachiosaurus* and *Euhelopus* in being slightly shorter and more massive, particularly the anterior half.

Dentary.—Dentaries preserved with the Marsh material from Como Bluff, Wyoming, include: YPM 1905 (p) (Fig. 43A, B), YPM 1910 (l), and an uncatalogued USNM specimen (r) from Quarry 13. Two right dentaries catalogued as AMNH 5761 (AMNH 5761 represented two or three individuals) are part of the Cope collection from Canon City, Colorado. From Bone Cabin Quarry, Wyoming, the American Museum of Natural History collected two pairs of dentaries, one belonging to the restored skull AMNH 467, and the other consisting of the isolated and separately catalogued AMNH 607 (r) and 657 (l). The Carnegie Museum of Natural History collected from Sheep Creek and Powder River, Wyoming, the dentaries CM 113 (r) and 312 (l), respectively. Seven skulls from Dinosaur National Monument have paired dentaries: CM 11338, 12020 (=11393), 11969, and 21751; USNM 13786; and DNM 28 and 975. Additional

isolated dentaries from the same quarry include DNM 4011 (r) of a very young individual, 4969 (r), and 21732 (l). The complete, well-preserved right dentary in DNM 975 has been removed, whereas the left remains in place and exposed medially. In DNM 1009 the left dentary is present but largely concealed by the medial jaw elements. Four isolated dentaries have been collected from the Cleveland-Lloyd quarry: UVP 1529 (r), 2655 (r), 3610 (r), and 3609 (l) (Fig. 44A–D). The anterior portion of UVP 2655 is complete to the level of the seventh alveolus, whereas the others are complete anteriorly through the entire tooth row, but in all four the thin lateral, plate-like posterior extension is incomplete. Lastly, a single, incomplete dentary, YPM 619, has been collected from Webster Park, Colorado.

The dentary is very massive and is among the most commonly preserved elements of the skeleton. It gradually attains its greatest depth anteriorly, terminating in a broad, flat symphysis. In lateral view the anterior margin recedes slightly posteroventrally. The lateral surface is generally convex and exhibits numerous small nutrient foramina, and, in at least DNM 975, three distinct, vertically oriented, groove-like channels occur near the anterior end. A narrow, shallow channel extends from about midlength of the ventral margin posterodorsally across its lateral surface to the sutural margin with the surangular. Below the channel the dentary thins noticeably in transverse section. The curvature of the dentary toward the symphysis begins at the level of its minimum vertical depth and the seventh alveolus. Posterior to the eighth or ninth alveolus the depth increases and the dentary bifurcates into a thin lateral and a much thicker medial plate-like process. The thin lateral plate has a very irregular posterior margin, the ventral portion of which continues posteriorly as a rectangular, lappet-like process that overlaps the anterior end of the angular. This portion of the dentary extends to about one-fourth of the distance to the posterior end of the jaw. The dorsal margin of this ventral process has a near-horizontal, narrowly underlapping contact with the surangular. Above the ventral process the much shorter portion of the lateral plate-like extension of the dentary overlaps the anterior end of the surangular in an irregular, vertical contact. The anterior end

of the surangular is firmly sutured between the lateral and medial plate-like posterior extensions of the dentary.

In medial view the Meckelian groove appears as a deep, U-shaped channel that abruptly narrows anteriorly as it extends along the ventral margin of the dentary. The channel is narrowest at the level of the seventh or eighth alveolus, then continues to the symphysis without change. At the point where the groove widens posteriorly the dentary divides into the lateral and medial processes, with the roof of the Meckelian groove being formed by the ventral margin of the medial process. The medial process of the dentary decreases in depth as it extends posterodorsally to overlap medially the anterior end of the surangular and form the anterodorsal border of the adductor fossa. The medial process ends in a blunt termination at or near the highest point on the posterior half of the jaw.

Viewed medially a series of 12 or 13 broad, deep alveoli are seen partially outlined along the dorsal margin of the dentary. The alveoli decrease in size posteriorly. Beneath them is a horizontal shelf which consists of the fused interdental plates and forms the dorsal margin of an alveolar groove that parallels the entire length of the tooth row. Below each alveolus the dorsal margin of the groove is perforated by an anteroposteriorly elongate, oval-shaped nutrient foramen that faces downward.

Comparison of the dentary of *Camarasaurus* with that in the prosauropod *Plateosaurus* reveals a number of marked differences. The dentary in *Camarasaurus* exhibits: 1) a significant shortening accompanied by major reduction in the number of teeth; 2) a stronger, medial symphyseal curvature, with a deepening and broadening of the symphysis; and 3) a generally greater massiveness. Among sauropods the dentary in *Brachiosaurus* is quite similar to that in *Camarasaurus*, but differs from it in: 1) having at least one more tooth, 2) being slightly less robust anteriorly, and 3) apparently not having the dorsal portion of the lateral process. Insofar as can be determined from several incomplete dentaries of juvenile specimens of *Pleurocoelus*, they also closely resemble that of *Camarasaurus* except in being less massive. The less massive dentition may be in great part a juvenile feature. The dentaries in *Euhelopus*, as in

Pleurocoelus, are similar to those in *Camarasaurus* but even less massive. A much greater contrast is evident between the dentaries in *Camarasaurus* and other sauropod genera with known dentaries: the diplodocids *Diplodocus*, *Barosaurus*, *Dicraeosaurus*, and *Nemegtosaurus*, and titanosaurid *Antarctosaurus*. In all five genera the dentary is more lightly constructed, and the dentition is far less massive. Further, in all of the above genera, except possibly *Barosaurus*, the dentary makes an abrupt medial bend anteriorly, giving the front of the jaw a squared-off appearance in dorsal view. The dentary referred to *Barosaurus* by Janensch (1935–1936) from the Tendaguru beds does not appear to be squared-off anteriorly, but this may be due to crushing. Further, the teeth in the five diplodocid genera are confined to the anterior end of the dentary, which in *Diplodocus* lies in a nearly transverse plane to the symphysis. The dentary in *Diplodocus* differs further from that in *Camarasaurus* in its small, medial symphysis being completely fused even in juveniles.

Surangular.—Paired surangulars are preserved in the skulls AMNH 467 from Bone Cabin quarry, and CM 11338, 11969, 12020, and 21751, DNM 28 and 975, and USNM 13786 from Dinosaur National Monument. The left surangular is present in DNM 1009, and incomplete surangulars are present in YPM 1905. Disarticulated surangulars from the Cleveland-Lloyd quarry include UUVF 3221 (r), 6820 (r), 10065 (l), 10795 (r), and 4027 (l). UUVF 6820 and 4027 are fragmentary, but the other four are nearly complete (Fig. 45).

For the most part the surangular forms a broad, anteroposteriorly oval plate that occupies a nearly vertical plane in the jaw. Posteriorly it is drawn out into a modest, tongue-like process with a rounded distal end. The anterior end of the surangular is firmly fitted into the very deep V-shaped notch of the posterior end of the dentary. The thick medial process of the dentary overlaps the dorsal area of the medial surface of the anterior third of the surangular; the shorter, thin lateral process of the dentary narrowly overlaps laterally the anterior portion of the ventral border of the surangular. The posterior portion of the ventral border of the surangular is overlapped laterally by the angular. The lateral surface is smooth and slightly bowed laterally except for a

very broad, shallow channel that extends postero-dorsally across its anterodorsal region. The channel is a continuation of that extending across the lateral surface of the dentary. The most prominent features on the medial surface of the surangular are two distinct, parallel, horizontal ridges on its broad, anterior oval portion. The flat area above the upper ridge is the sutural surface for the thick, posterodorsally directed, medial process of the dentary, whereas the slightly concave area below the lower ridge is the sutural surface for the prearticular. Below the lower ridge the ventral portion of the posterior, tongue-like process of the surangular curves medially so as to sheath both the lateral and ventral surfaces of the articular. A large, oval foramen lies in the center of the anterior plate-like portion of the right and both surangulars of DNM 975 and CM 11338, respectively, and is present, but noticeably smaller, in UUV 3221 and 10795.

The surangular in *Camarasaurus* is like that in *Brachiosaurus* except for its anterior end being less overlapped by the lateral process of the dentary, resulting in a greater lateral exposure. The surangular in *Euhelopus* also appears to be very similar to that in *Camarasaurus*, although its sutures with the dentary and angular in the one known specimen are obliterated. Similarities are also evident between the surangulars in *Camarasaurus* and *Nemegtosaurus* except that in the latter there is no prominent channel extending postero-dorsally across its lateral surface, and the posterior tongue-like process is much shorter, so that the dorsal margin of the mandible rises much more steeply from the posterior end. In these same ways the surangular in *Plateosaurus* differs from that in *Camarasaurus*. The surangular in *Diplodocus* is quite different from that in *Camarasaurus* in that the anterior oval plate is much narrower and longer, resulting in the posterior two-thirds of the jaw varying little in height except at the posteriormost end. Also in contrast to the condition in *Camarasaurus* the upper portion of the surangular flares laterally in the articular region, rather than maintaining its otherwise vertical plane. In *Camarasaurus*, on the other hand, the plane of the surangular in this region slopes dorsomedially.

Angular.—In addition to the angulars in YPM

1907 and AMNH 467, and in the three articulated mandibles from Dinosaur National Monument mentioned above, a disarticulated angular UUV 10068 (1) (Fig. 46) is also known from the Cleveland-Lloyd quarry.

The angular is an elongate, solidly built element which occupies the ventral posterior two-thirds of the jaw. Its blade-like anterior half, which tapers to a blunt point, occupies a plane that slopes ventromedially about 30° from the vertical. The height of the blade-like anterior portion increases to about midlength of the element, then decreases somewhat in height more posteriorly. The posterior half of the angular is composed of vertical and horizontal laminae that meet to form between them a dorsomedial right angle. The anterior portion of the angular is overlapped laterally by the dentary and medially by the splenial, so that the ventral edges of all three elements run parallel to each other along the middle third of the ventral margin of the jaw. Posteriorly the laterally exposed, vertically oriented lamina of the angular thins greatly dorsally as it laterally overlaps and fits into a step-like depressed area along the ventral margin of the surangular. The horizontal, medially directed lamina of the posterior half of the angular forms the floor of the adductor fossa.

A prominent ridge runs the entire midmedial length of the angular. It gradually becomes most pronounced as it is traced posteriorly for about two-thirds of its length, where it then decreases in height and thins gradually to a sharp edge to the posterior end of the bone. Just above this ridge is a broad, shallow groove which deepens substantially posteriorly beyond the midlength of the angular. Below the ridge on the posterior half of the angular is a second, more flattened groove which received the prearticular. The very slightly convex surface below the groove on the anterior half of the angular articulates with the lateral surface of the splenial.

The angulars in *Camarasaurus* and *Brachiosaurus* are virtually indistinguishable, and, as far as can be determined, those in *Camarasaurus* and *Euhelopus* are quite similar. The angular in *Pleurocoelus* is also quite similar to that in *Camarasaurus*, but a little narrower. No disarticulated angulars are known in *Diplodocus*, and the medial

face is largely covered by the prearticular. Judging from the exposed surfaces in articulated jaws, it is clear that the angular is oriented much more vertically in *Diplodocus* than in *Camarasaurus*. The jaw in *Diplodocus* is extremely thin mediolaterally, and the large Meckelian canal, which extends the length of the jaw in such forms as *Camarasaurus* and *Brachiosaurus*, must be greatly reduced or more likely absent. It appears that Nowinski (1971) has mistaken the prearticular for the median surface of the angular in *Nemegtosaurus*, and until this question is clarified comparison cannot be made. The angular in *Plateosaurus* occupies a vertical plane and thus more closely resembles that in *Diplodocus* than that in *Camarasaurus*.

Preaticular.—Of the five known prearticulars of *Camarasaurus*, three are disarticulated but incomplete and include a left (Fig. 47D, E) and right (Fig. 47A–C) of the skulls DNM 28 and 975, respectively, and the isolated left UUVP 5073. In addition, the medial surface is exposed in the complete right prearticulars of skulls DNM 975 and 1009, and the left of the disarticulated skull CM 11969. The complete prearticulars of the articulated skull CM 11338 are exposed in medial view. The prearticular in DNM 28 was found disarticulated and was misidentified and figured by White (1958) as the vomer.

In general, the prearticular has the form of an elongate, vertical, thin plate. Whereas the ventral margin is nearly straight, the central portion of the dorsal margin is expanded into a high, broadly convex flange. The concave portion of the dorsal margin extending between the crest of the convex central flange and the slightly expanded anterior end forms the medial border of the adductor fossa. A ridge near the ventral margin of the lateral surface extends posteriorly a third of the length of the prearticular. The ridge parallels the convex dorsal margin to within a short distance of the posterior end of the prearticular. Here the ridge becomes continuous with the lateral edge of a horizontal, blade-like process of the posterior end of the prearticular that ventrally supports the articular. The expanded anterior end of the prearticular is overlapped medially by the coronoid and splenial, and laterally by the dentary. The anterior third of the ventral margin of the prearticular is paper thin and medially overlapped by an

equally thin margin of the splenial. More posteriorly the angular overlaps the central third of the ventral margin of the lateral surface beneath the ridge, then unites with the ventral surface of the blade-like posterior process of the prearticular.

The prearticulars in *Camarasaurus* and *Brachiosaurus* are very similar except for that of the former being relatively slightly shorter. The prearticular in *Diplodocus* resembles in general that in *Camarasaurus*, differing mainly in being a virtually flat plate of bone of much greater uniform height throughout its length. The disarticulated prearticular is not known in any other advanced sauropod. In *Brachiosaurus* the general shape and relationships of the prearticular to adjoining elements is similar to that in *Camarasaurus*, but is much more narrow, with its dorsal margin rising little above the lower rim of the jaw. Consequently the adductor fossa opens mainly medially rather than dorsally.

Articular.—Of the six known *Camarasaurus* articulars, the best preserved is an isolated left from the Cleveland-Lloyd quarry, UUVP 4939 (Fig. 48D–F). Another disarticulated but slightly imperfect specimen belonging to YPM 1907 was illustrated under Marsh's direction, but the figures were never published and appear here for the first time (Fig. 48A–C). Dorsal views of the articular are available in the articulated mandibles of the two skulls exposed on the quarry face at Dinosaur National Monument, DNM 975 and 1009. Additionally, although both articulars are present in the articulated skull CM 11338, they are not fully exposed and provide little information beyond the shape of the articular surface.

The massive block-like articular is over twice as long as it is wide and generally wider than high. It lies tightly cradled between the surangular laterally, the angular ventrally, and the prearticular medially. A shallow trough-like depression on the medial surface accommodates the prearticular, whereas the lateral articulation with the surangular is rather flat except for a pronounced concavity just in front of the bluntly rounded distal end. A well-developed rounded ridge runs the midventral length of the bone. In dorsal view the articular widens very rapidly from the posterior end, attaining a maximum width which is maintained for three-quarters of its length. The medial and

lateral surfaces meet anteriorly in a 60° angle between them, as do the converging surangular and prearticular bones sheathing these surfaces of the articular. The dorsal surface is rugose, with the front half providing the articular surface for the quadrate. At the posteromedial rim of the articular surface a dorsal triangular projection rises abruptly.

The articular in *Brachiosaurus* contrasts sharply with that in *Camarasaurus* in that it is wedge-shaped posteriorly. In *Diplodocus* it differs even more greatly in having a nearly flat dorsal surface and a sharp, deep ventral keel. The much more complex articular in *Plateosaurus* is distinctly different, most notably in having a pronounced medial projection.

Splenial.—The rarely preserved sauropod splenial is known to be complete in only two specimens of *Camarasaurus*, although fragmentary remains are present in several others. Fortunately, the paired splenials of both specimens are complete and well preserved. Of a pair belonging to DNM 975, the left is exposed in medial view and the right is completely freed (Fig. 49). The second pair is exposed in medial view in the articulated lower jaws of CM 11338.

The splenial is a very thin, nearly flat lamina of bone oriented vertically on the medial surface of the jaw. The splenial can be divided into two components: 1) a dorsoventrally narrow, anteroposteriorly elongate band that extends along the ventral border of the jaw; and 2) a broad flange that extends dorsally from the dorsal margin of the ventral band, dividing the band into anterior and posterior processes. The posterior end of the ventral margin of the ventral band extends along the ventral border of the jaw for a short distance, then gradually retreats a short distance from the ventral margin as it continues anteriorly. The ventral band is bowed medially, particularly its posterior process, which overlaps the medial surface of the angular. The posterior process terminates in an irregular indentation that produces two very small, posteriorly directed processes of which the dorsal is larger and pointed. The straight dorsal margin of the posterior process parallels, but is narrowly separated from, the ventral margin of the anterior end of the prearticular. The nearly vertical basal portion of the posterior margin of

the dorsal flange medially overlaps the anterior end of the prearticular. The slightly concave dorsal portion of the posterior margin of the dorsal flange above the prearticular–splenial suture contacts the coronoid in an abutment suture. The anterodorsal margin of the dorsal flange is very slightly convex and contacts the ventral margin of the intercoronoid. An anterior elongation of the dorsal flange produces a narrow gap between it and the anterior process of the ventral band, which partially exposes the anterior end of the Meckelian canal in the dentary. The narrow, splint-like anterior process of the ventral band tapers to a point as it inserts along the ventral rim of the Meckelian channel of the dentary.

Other than its principal suture with the angular, the greater part of the lateral surface of the splenial contacts the dentary. The lateral surface is essentially flat except for a distinct channel that extends the length of the ventral band. The channel is the full width of the posterior process of the band and is occupied completely by the articulating angular. For the remainder of its length anteriorly the channel steadily narrows as its ventral border converges on the anterior end of the dorsal margin of the anterior process. This part of the channel appears to form a very narrow portion of the ventromedial wall of the Meckelian channel. In two specimens of *Camarasaurus*, AMNH 567 and 5761, White (1958:489) described what he interpreted to be “the splenial extending forward as a small sliver of bone on the ventromedial side of the dentary to take part in the symphysis.” Examination of these specimens confirms White’s observation. This is in sharp contrast with the much shorter anterior process of the splenials in CM 11338, which end far short of the symphysis. The difference in the development of the anterior process of the splenial may reflect a difference in growth, inasmuch as the much smaller CM 11338 represents a juvenile.

Complete splenials are known in *Brachiosaurus*, *Diplodocus*, and *Nemegtosaurus*, and only a fragmentary splenial is known in *Antarctosaurus*. They all generally resemble that in *Camarasaurus*, with some variation in shape. Whereas the splenial in *Brachiosaurus* may extend to the symphysis, those of the other three genera appear to terminate before the symphysis. The splenial in *Plateosaurus*

is remarkably like that in *Camarasaurus* and may also send an anterior splint-like process to the symphysis.

Coronoid.—Recent preparation of the medial surfaces of the left jaw of DNM 975 and those of CM 11338 has revealed for the first time an element believed to be the coronoid (Fig. 41B). Although the medial surface of the left mandible of CM 11338 is poorly preserved in the area of the coronoid, a fragment of it appears to be present. In his description of CM 11338 Gilmore (1925) described a coronoid, but it is obvious that he was inferring its presence on the lateral surface of the jaw. The element identified here as the coronoid is very small and lies at the anterior end of the adductor fossa on the medial surface of the jaw.

The coronoid, the smallest element of the jaw, is slender, mediolaterally flattened, and roughly crescentic in outline. Its concave posterior margin borders the anterior margin of the adductor fossa. Its convex anterior margin abuts against the dorsal flange of the splenial except for a small section of its dorsalmost end which contacts the ventral margin of the intercoronoid. The coronoid overlaps the medial surfaces of the dentary dorsally and the prearticular ventrally.

The coronoid in *Camarasaurus* is nearly identical to that described by Brown and Schlaikjer (1940) for *Plateosaurus* (AMNH 6810). In *Plateosaurus*, however, it extends posterodorsally to overlap medially the uppermost level of the anterior end of the surangular. McIntosh and Berman (1975) were unable to recognize a coronoid in the jaw of *Diplodocus* CM 11161. Many of the sutures of this adult specimen, however, are very indistinct, and the element is believed to be probably present. The same is probably true in *Brachiosaurus*, although Janensch (1935–1936) was also unable to detect a coronoid. The coronoid has been identified, however, in two other saurpods, *Antarctosaurus* and *Nemegtosaurus*. Only the anterior half of the jaw is known in the former, with the break passing through the coronoid. As determined by Huene (1929), the anterior end of the coronoid lies at the dorsalmost level of the jaw, medially overlapping the contact between the dentary and surangular. Ventrally it has an extensive suture with the splenial, as in *Camara-*

saurus. A complete coronoid is apparently known in *Nemegtosaurus*, but its anterior suture with the dentary could not be delineated by Nowinski (1971). Posteriorly it overlaps the medial surface of the surangular, whereas ventrally it contacts the splenial, but the extent of this suture has not been determined.

Intercoronoid.—The intercoronoid has not been previously reported in *Camarasaurus*, although it has been recognized in *Brachiosaurus* by Janensch (1935–1936), who referred to it as the “complementare.” A homologous bone has been described in the theropods *Allosaurus*, *Ceratosaurus*, and *Tyrannosaurus* by Madsen (1976), Gilmore (1920), and Osborn (1912), respectively. Believing that the element was derived from the splenial, Osborn (1903) termed it the “presplenial” in his description of the skull of *Creosaurus* (= *Allosaurus*), only to later rename it the “supradentary” in his (1912) description of *Tyrannosaurus*. The term “supradentary” was applied to the homologous element in *Antrodemus* (= *Allosaurus*) and *Ceratosaurus* by Gilmore (1920). Brown and Schlaikjer (1940) recognized the intercoronoid in such diverse dinosaurs as the prosauropod *Plateosaurus*, the ceratopsians *Protoceratops* and *Triceratops*, and *Tyrannosaurus*, and considered it homologous with the intercoronoid of amphibians and some primitive reptiles. Finally, Madsen (1976) applied the name intercoronoid in preference to supradentary in his description of *Allosaurus*.

The intercoronoid, as preserved in CM 11338 (Fig. 41B, C) and DNM 975 (Fig. 42A, B), is a long, narrow, thin sheet of bone that medially sheaths the interdental plates along the lingual bases of the tooth row from about the fourth tooth to near the posterior end of the series. The middle third of the bone ventrally contacts the splenial.

As far as can be determined, the intercoronoid in *Camarasaurus* most closely resembles that in *Brachiosaurus*. In both genera the element extends much farther forward and sheaths more of the tooth row than in *Plateosaurus*. The intercoronoid in *Plateosaurus* is also extremely narrow. An intercoronoid has not been identified in any diplodocid, and there is some question as to whether it existed in this highly specialized group. McIntosh and Berman (1975) failed to detect it in the unusually complete skull of *Diplodocus* CM

11161. On the medial surface of the dentary of that specimen the nutrient foramina beneath the alveoli, which might be expected to be covered by the intercoronoid, are clearly visible. The same is true in *Nemegtosaurus*, and Huene (1929) failed to see any indications of the intercoronoid in the jaw of *Antarctosaurus* in which the other medial elements of the jaw were preserved.

DENTITION

Gilmore (1925) described the *Camarasaurus* skull CM 11338 as having four teeth in each premaxilla, eight teeth in the left and nine in the right maxilla, and 13 teeth in each dentary. The number of maxillary teeth in *Camarasaurus* appears to vary. Four Cleveland-Lloyd specimens, UVP 1859, 1860, 3454, and 4005, have nine maxillary teeth, whereas DNM 28 has ten teeth in both maxillae. On the other hand, the four premaxillary and the 13 dentary teeth appear to be constant, although a variation of one in some specimens would not be unexpected. The description of the teeth has been treated exhaustively by White (1958) and also Carey and Madsen (1972) and needs no further discussion here.

HYOID

Gilmore (1925) reported the presence of three rod-like elements found beneath the lower jaw of CM 11338. These are clearly elements of the hyoid arch. He interpreted two of these, which are paired, as probably thyrohyals. Little else can be added to Gilmore's (1925) description of these bones.

ATLAS-AXIS COMPLEX

Because the atlas-axis complex is very rarely preserved, is the only inadequately known postcranial region of *Camarasaurus*, and has potential systematic importance, a brief description is given here.

Proatlas.—The proatlas is known only in *Camarasaurus grandis* YPM 1905 (paratype, Fig. 50) and AMNH 467. The paired elements were first identified in a sauropod by Marsh (1883), who referred to them as the "post-occipital bones" in a small sauropod USNM 5384 that he (Marsh, 1889b) later identified as *Morosaurus agilis*. The

specimen was subsequently described in detail by Gilmore (1907), but as already noted above, we believe that it probably does not pertain to *Camarasaurus*. The proatlas of *C. grandis* YPM 1905 was figured by Ostrom and McIntosh (1966:pl. 3, fig. 4) and erroneously identified as the postfrontal(?) of YPM 1912.

As nothing pertinent can be added to Marsh's (1883:82–83) original description of the proatlas, it is repeated here:

When in place [these bones] are attached to the occiput just above the foramen magnum and extend backward and outward, overlapping the lateral pieces [neuropophyses] of the atlas thus protecting the spinal cord at this point, which would otherwise be very much exposed. The bones are short, flattened and slightly curved, resembling somewhat a riblet. The anterior end is thickened and rugose for the attachment to a roughened surface of the exoccipital just above the outside the foramen magnum. The shaft is flattened from above downward, and gradually converges to a thin posterior end. In *Morosaurus grandis* [YPM 1905] these bones are about 65 mm. in length, and 30 along the surface which joins the occiput.

Atlas.—The atlas is preserved in position in several articulated skeletons (CM 11338, AMNH 467, USNM 13786, and with the skull of DNM 1009) and disarticulated in numerous other specimens (YPM 1905, 1907; DNM 28; UVP 2983, 3417, 3467, 4016, 10070).

The atlas consists of the intercentrum and paired neuropophyses (Fig. 51, 52). In about half of the specimens examined the neuropophyses and intercentrum are firmly fused. In lateral view the paired neuropophyses have the appearance of posterodorsally directed, wing-like structures. When fused to the intercentrum they closely approach one another distally along the midline but never make contact. An oval facet for the proatlas is located at the anterior end of the dorsal surface of the neuropophysis. At about midlength along the ventral surface of the neuropophysis is a prominent, oval articular facet for the prezygapophysis of the axis. In end views the bases of the neuropophyses are expanded medially to form the lateral margins of a subcircular channel into which the odontoid process of the axis projects. Above this the neuropophyses form the deeply concave lateral margins of the neural canal. In end views the intercentrum has the shape of a broad crescent,

with the apices directed dorsomedially. Its transverse diameter is almost twice its longitudinal length. The anterior surface is concave for articulation with the occipital condyle, whereas the posterior surface is convex. Pleurocoels are absent, and a flattened area near the posteroventral margin of the lateral surface is the facet for a single-headed rib. A broad, rugose, anteroposteriorly oval articular facet for the neurapophysis is located very near the dorsomedial margin of the intercentrum, so as to face principally dorsally and slightly laterally.

Axis.—In addition to those of articulated skeletons (AMNH 467; CM 11338; DNM 975, 1009; USNM 13786), axes are present in several disarticulated specimens (AMNH 5761; CM 11969; DNM 28; UUV 1555, 4273, 6341; YPM 1905, 1907, 1910) (Fig. 53).

The neural arch extends the full length of the centrum, and the halves are apparently always strongly fused, even in the juvenile holotype of *C. lentus* (YPM 1910). Well-developed diapophyses project directly laterally from about midlength of the neural arch and just above its contact with the centrum. Small prezygapophyses for articulation with the neurapophyses of the atlas are located on the dorsal end of the anterior margin of the pedicels. The neural arch expands in transverse width

posteriorly, and its well-developed, nondivided neural spine increases in height as it extends the full length of the arch. The articular planes of the strongly developed postzygapophyses are inclined somewhat ventromedially. The axial centrum consists of the always fused true centrum and intercentrum (Gilmore, 1907), and the prominent odontoid process (=pleurocentrum of the atlas). Together the true axial centrum and intercentrum resemble the atlantal centrum (consisting of only the intercentrum) except in being considerably longer. As in the atlas, the axial intercentrum is crescent-shaped in anterior view. The odontoid process is fused immovably within the space of the crescent on the upper half of the anterior surface of the intercentrum. In lateral view the odontoid process has roughly the outline of an isosceles right triangle, with the hypotenuse forming the anteroventral side and meeting the dorsal, horizontal side anteriorly in a blunt apex. The opening of a prominent pleurocoel extends over more than half of the lateral surface of the centrum. The parapophysis is located near the anteroventral margin of the lateral surface of the centrum.

The third cervical of *Camarasaurus* sp. UUV 10896 is figured here (Fig. 54), but without description.

TAXONOMIC HISTORY

During the summer of 1877 O. W. Lucas collected a number of bones of a very large dinosaur in the uplands just west of and overlooking the southern end of Garden Park, 13 km north of Canon City, Colorado. These fossils, which came from the top of the Upper Jurassic Morrison Formation (Osborn and Mook, 1921), were sent to E. D. Cope in several shipments during the summer and autumn of that year. On the basis of the material received in the first shipment, consisting of a cervical, two dorsals, and four caudal vertebrae, Cope (1877a) described the new genus and species *Camarasaurus supremus*. As later shipments were received, he added to the diagnosis of the species (Cope, 1878). The material later proved to be parts of two very large individuals of about the same size, representing

most of the postcranial skeleton except the forelimb, fore and hind feet, and all of the cervicals but the one already noted. These fossils came from what Osborn and Mook (1921) designated as Cope Quarry No. 1. When, after Cope's death, his collection was transferred to the American Museum of Natural History, the material was catalogued as AMNH 5760. A second shipment from O. W. Lucas contained various remains from a nearby, although different, quarry or quarries at about the same stratigraphic horizon. This collection included a series of large spatulate teeth (AMNH 5768) which formed the basis of Cope's (1877b) description of *Caulodon diversidens*. Cope (1878) later named a second species of *Caulodon*, *C. leptogonus*, based on a single tooth from a quarry distant from Cope Quarry No. 1.

At about the same time O. W. Lucas was collecting in Colorado, W. H. Reed and W. E. Carlin discovered a Morrison Formation locality containing dinosaur bones on the north side of Como Bluff, Wyoming, a short distance south of the railroad station at Lake Como on what was then the main line of the Union Pacific Railroad. These were sent to O. C. Marsh and included, among other specimens, a series of articulated caudal vertebrae, a dorsal vertebra, and two femora of different sizes. They were described by Marsh in December 1877 as a second new species of *Apatosaurus*, *A. grandis*, for which the type species, *A. ajax*, is based on the greater part of a much larger skeleton collected at Morrison, Colorado.

In the meantime, Marsh had sent his young assistant S. W. Williston to Como Bluff to supervise and assist Reed and Carlin in the collecting. A number of shipments were made to Marsh from this quarry, designated as YPM-Marsh Quarry 1 (Ostrom and McIntosh, 1966), during the winter of 1877–78. Among the bones received in these later shipments was the greater part of a sacrum (YPM 1900) on which Marsh (1878a) based the genus and species *Morosaurus impar*. Eight months later, as the material from the quarry was prepared, Marsh (1878b) referred *Apatosaurus grandis* to *Morosaurus* as *M. grandis*. Although Marsh later realized that *M. grandis* and *M. impar* were conspecific, he never published this, perhaps because he had figured the holotypic sacrum of the latter under the former name. In the same paper he applied the new name *Morosaurus robustus* to an ilium (YPM 1902) from the same YPM-Marsh Quarry 1. This was supposedly a larger species than *M. grandis*. In the field Williston had recognized that most of the bones from the quarry belonged to two skeletons of about the same size and applied to them the field designations Δ and Φ , but were later catalogued as YPM 1901 and 1905, respectively. The two skeletons have sometimes been considered as cotypes of *M. grandis*, but since no parts of YPM 1905 were at hand when Marsh described "*Apatosaurus*" *grandis*, it seems more appropriate to designate YPM 1901 as the holotype and YPM 1905 as the paratype.

Judging from the complete collection of bones from YPM-Marsh Quarry 1, several quite explicit

quarry maps of the earlier excavations of Carlin, and sketchy diagrams drawn by Williston during later excavations, one can now state that no fewer than four individuals of the same species of *Camarasaurus* were present. YPM 1901 and 1905 were, as already stated, represented by large portions of two skeletons of comparable size, and were only partially articulated and their bones somewhat intermingled, so that it is not always possible to be sure of assignments of the elements. Recognizing these limitations and noting that there are some differences from the assignments given in "Marsh's Dinosaurs" (Ostrom and McIntosh, 1966) compared to the numbers drawn on the bones, the most likely separation of the two specimens is as follows: YPM 1901 (holotype of *M. grandis*), includes basioccipital, several dorsal vertebrae, ribs, partial sacrum, articulated caudal vertebrae 1–27, and perhaps nine, disarticulated others, left pectoral girdle and forelimb with one carpal and metacarpal III, right scapulocoracoid, left sternal plate, and both femora; and YPM 1905 (paratype of *M. grandis*) includes skull and mandible, cervical vertebrae 1–12, most or all of the dorsal vertebrae, incomplete sacrum, at least 12 caudal vertebrae and possibly others, ribs, chevrons, scapulocoracoids, left humerus, right ulna, ?ilia, right ischium, femora, tibiae, fibulae, and greater parts of pedes.

In addition to the above two specimens, some disarticulated elements belonging to a smaller individual, including a right scapula and left pubis, were catalogued as YPM 1903. The holotypic sacrum YPM 1900 of *M. impar* is the same size and very likely belongs to the same individual as do the incomplete, paired coracoids and ischia, several vertebrae, and left femur that was part of the first shipment from the YPM-Marsh Quarry 1 and whose measurements were given in the original description of "*Apatosaurus*" *grandis* by Marsh (1877). Ironically, the other femur sent in that shipment, a right element not mentioned in the paper, undoubtedly belongs to YPM 1901. In addition, the ilium assigned by Marsh to YPM 1901 may belong to the smaller individual, YPM 1903, whereas the ilium YPM 1902, the holotype of *M. robustus*, belongs to either YPM 1905 or a fourth individual that is slightly larger than any of the others. After Williston returned to Yale Pea-

body Museum, Reed recovered a femur and caudal vertebrae from near to the other specimens of YPM-Marsh Quarry No. 1 which probably belong to either YPM 1905 or an as yet unidentified individual.

O. W. Lucas and his brother I. A. Lucas continued to send Cope a number of shipments of specimens from Garden Park, Colorado, over the next several years, none of which were ever opened during Cope's lifetime. Several boxes contained specimens from Cope Quarry No. 2 (Osborn and Mook, 1921) which, when eventually opened and prepared in New York, were found to contain a maxilla, quadrate, partial pterygoid, braincase, and two right dentaries. All of the bones from Cope Quarry No. 2 were catalogued as AMNH 5761, although they represent two specimens, as well as probably a third large individual, of *Camarasaurus supremus*. Although the quarry is quite near to and at the same horizon as Cope Quarry No. 1, the specimens are best considered as topotypes. Finally, Cope (1879) described a second species of *Camarasaurus*, *C. leptodirus*, based on three cervical vertebrae subsequently catalogued as AMNH 5763. Although it is not known from what quarry they were collected, it was almost certainly not Cope Quarry Nos. 1 or 2.

Marsh (1889b) described briefly two new species of *Morosaurus*. One, *M. lentus*, was based on the greater part of the postcranial skeleton and some fragments of the skull and jaw of a very juvenile specimen (YPM 1910) found in the

famous *Stegosaurus* quarry, YPM-Marsh Quarry 13, 4 mi east of Como Bluff, Wyoming. The other new species, *M. agilis*, was based on a basicranium and the first three cervicals (USNM 5384, originally YPM 1904) from the YPM Marsh-Felch Quarry 1 in Garden Park, Colorado. This specimen does not belong to *Camarasaurus* (JSM, personal observation) and, therefore, will not be discussed further. Additionally, Sauvage (1897/8) described a vertebra from the Upper Jurassic of Portugal as *Morosaurus marchei*, but this specimen is now known to be a megalosaurid (JSM, personal observation).

On the basis of a series of five posterior cervicals (CM 11069) collected from the Dinosaur National Monument quarry by Carnegie Museum of Natural History, Holland (1919) named without description *Uintasaurus douglassi*. In 1924 he not only described the vertebrae, but referred a second specimen (CM 11373, now USNM 13786), consisting of a complete skeleton except for the tail, to this species. *Uintasaurus douglassi* is clearly referable to *Camarasaurus*, as noted by White (1958). Finally, Ellinger (1950) described *Camarasaurus annae* on the basis of an anterior dorsal vertebra (CM 8942) also from Dinosaur National Monument. The features cited as distinguishing this species are undoubtedly due to individual variation, since other dorsals found with the holotype and clearly belonging to it do not exhibit them (McIntosh, 1981).

SYSTEMATICS

It is not our intention to present a detailed classification of the Sauropoda, as such was recently presented by McIntosh (1990b). In addition, because many genera are incompletely known, a meaningful analysis of relationships at this time would be impossible. Most importantly, however, such an analysis would require considerable discussion of postcrania, which is not treated here. The intention here is to present an updated diagnosis of the family Camarasauridae and the genus *Camarasaurus*, as well as comment on several forms which have been variably referred to Camarasauridae.

The Portuguese species "*Apatosaurus*" *alenuquerensis* Lapparent and Zbyszewski, 1957, should undoubtedly be placed in Camarasauridae and has been tentatively referred to *Camarasaurus* (McIntosh, 1990a, 1990b). Its most obvious difference from the American species is a greater humero-femoral length ratio. Although eventually it may be determined that it represents a new genus, the absence of the skull and highly diagnostic presacral neural arches and spines, and the possibility that it may be closely related to the incompletely known Spanish camarasaurid *Aragosaurus* (Sanz et al., 1987) make assignment imprudent at this

time.

Two Asiatic genera have also been questionably referred to Camarasauridae (McIntosh, 1990a, 1990b). *Euhelopus* from the Late Jurassic of China possesses a *Camarasaurus*-like skull, but unfortunately the partial and only known skull of this genus lacks three of the most diagnostic elements—the nasals, jugals, and vomers. The posterior cervicals appear to exhibit incipient division of the neural spines, a feature which is very pronounced in *Camarasaurus*. The tail is unknown, and the forelimb and girdle, believed to be represented by a scapulacoracoid and humerus, were collected several years after the initial discovery of the holotype and may not belong to it. Thus, the important humero-femoral length ratio is uncertain. On the other hand, its large number of presacral vertebrae casts doubt on a Camarasauridae assignment. Therefore, the discovery of additional material is necessary before the affinities of *Euhelopus* can be confidently determined.

The relationships of *Opisthocoelicaudia* Borsuk-Bialynicka, 1977, from the Late Cretaceous of Mongolia are even more problematic. Unfortunately, the skull and neck are unknown. Its age, however, suggests a possible association with Titanosauridae, as do some features of the limbs and girdles, particularly the pelvis (McIntosh, 1990b). On the other hand, the neural spines of the anterior dorsal vertebrae are deeply divided with the typical camarasaurid, U-shaped cleft, which is not seen in titanosaurids. Further, the caudal vertebrae of *Opisthocoelicaudia* are strongly opisthocoelous and, therefore, easily contrasted with the characteristically strongly procoelous caudals of Titanosauridae.

Osborn and Mook (1921) referred *Morosaurus* Marsh, 1878, and *Caulodon* Cope, 1877, to *Camarasaurus* Cope, 1877. Similarly, White (1958) referred *Uintasaurus* Holland, 1919, to *Camarasaurus*. We concur with these reassignments. Of the two species of *Camarasaurus* erected by Cope, Osborn and Mook (1921) referred *C. leptodirus* to the type species *C. supremus*. The holotypic specimens of the three species of *Morosaurus* erected by Marsh (1877, 1878a, 1878b), *M. grandis*, *M. impar*, and *M. robustus*, were all found intermingled in the same

quarry at Como Bluff, and it is reasonable, therefore, to assume that they represent a single species. *Morosaurus lentus*, the holotype of which came from a different Como Bluff quarry and the species to which most of the *Camarasaurus* specimens from Dinosaur National Monument have been referred, is probably distinct from *C. grandis*, but in our opinion has not yet been satisfactorily separated from *C. supremus*. *Morosaurus agilis* Marsh, 1889b, probably does not pertain to *Camarasaurus* and for that reason is not treated here. Finally, the poorly known *C. annae* Ellinger, 1950, is inseparable from other *Camarasaurus* species from Dinosaur National Monument. Although there is postcranial evidence supporting the validity of at least two *Camarasaurus* species from North America, *C. supremus* (including possibly *C. lentus*, but is here retained provisionally) and *C. grandis*, their crania are indistinguishable; the potential controversy is left unresolved here. Although the excellently preserved forelimb of *Pelorosaurus becklesii* Mantell, 1852, from the English Wealden was often referred to *Morosaurus* by Marsh (1889a) and *Camarasaurus* by Huene (1932), the evidence for either assignment is far from conclusive.

Family Camarasauridae Cope, 1877

Revised Diagnosis.—Skull: Shortened muzzle; quadrate nearly vertical and robust; jugal excluded from ventral margin of skull; basiptyergoid processes short; large nares positioned anteriorly; teeth broad and spatulate. Vertebral column: presacral vertebrae have prominent pleurocoels, with those of the cervicals being complex; neural spines divided in shoulder region and relatively low in posterior dorsals; presacral centra strongly opisthocoelous; tail relatively short; caudal vertebrae short and lack pleurocoels; chevrons only moderately developed, with no fore-and-aft expansions of distal ends; diapophyses of anterior caudals simple knobs. Appendicular skeleton: forelimb to hindlimb length ratio value moderate, intermediate between those for the longer and shorter forelimbed brachiosaurids and diplodocids, respectively; metacarpals long and slender; metatarsal I lacks process on posteroventral margin of lateral surface; metatarsals II and III longest rather

than III and IV as in diplodocids.

Included Genera.—*Camarasaurus*, *Aragosaurus*, and possibly *Euhelopus*, and/or *Opisthocoelicaudia*.

Genus *Camarasaurus* Cope, 1877

Revised Diagnosis.—Jaws massive; vomer massive; 12 cervical and 12 dorsal vertebrae; presacral neural spines well developed and divided from about cervical 4 posteriorly to middorsal region or farther, depending on age; notch of divided spines U-shaped rather than V-shaped as

in diplodocids; neural spines of posterior dorsals, sacrals, and anterior caudals short and massive, and expanded transversely into massive ball-like structures; sacral centra solid; sacral spines 2–5 tend to fuse to each other; short tail of 53 vertebrae; distal end of scapular blade broadly expanded; forelimb bones slender; humero-femoral length ratio ~0.77; two carpals; metacarpal III to humerus length ratio ~0.33; pubis massive with short shaft; ischium very slender with unexpanded distal end; hindlimb bones massive; tibiofemoral ratio ~0.60; small spheroidal calcaneum.

ACKNOWLEDGMENTS

As always in a study of this kind, it is impossible to recognize fairly all those who have contributed generously of their time and knowledge. We do, however, want to acknowledge our gratitude to the following individuals who have expedited our efforts by contributing encouragement and/or data: the late Ted White, who originally urged the restudy of Dinosaur National Monument material and encouraged a more comprehensive investigation than was possible at the time of his study; Russell King, who collaborated in the early stages of the project, but was a victim of an untimely accident; Dan Chure, whose aptitude, enthusiasm, and assistance are what make the collection at Dinosaur National Monument the valuable resource that it is; and Paul Sereno, whose critical reading of an early version of the manuscript provided many helpful comments and suggestions.

Beyond the initial collection of the specimens, it is their

preparation that has obviously been the real key to the success of this project, and for that reason special thanks are due Allen McCrady of the Carnegie Museum of Natural History and Tobe Wilkens of Dinosaur National Monument, whose talents and cooperation have been a most essential part in providing that all-important better look at the various specimens.

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LITERATURE CITED

- BERMAN, D. S., AND J. S. MCINTOSH. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of Carnegie Museum of Natural History* no. 8, 35 pp.
- BORSUK-BIALYNICKA, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n. sp. n., from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica*, 37:5–64.
- BROWN, B., AND E. M. SCHLAICKER. 1940. A new element in the ceratopsian jaw with additional notes on the mandible. *American Museum Novitates* 1092, 13 pp.
- CAREY, M. A., AND J. H. MADSEN, JR. 1972. Some observations on the growth, function, and differentiation of sauropod teeth from the Cleveland-Lloyd Quarry. *Utah Academy Proceedings*, 49(1):41–43.
- COLBERT, E. H., AND J. H. OSTROM. 1958. Dinosaur stapes. *American Museum Novitates* 1900, 20 pp.
- COPE, E. D. 1877a. On a gigantic saurian from the Dakota Epoch of Colorado. *Paleontological Bulletin*, 25:5–10.
- _____. 1877b. On reptilian remains from the Dakota beds of Colorado. *Paleontological Bulletin* 26, reprinted in *Proceedings of the American Philosophical Society*, 17: 193–196 (1878).
- _____. 1878. On the Vertebrata of the Dakota Epoch in Colorado. *Paleontological Bulletin* 28, reprinted in *Proceedings of the American Philosophical Society*, 17: 233–241.
- _____. 1879. New Jurassic Dinosauria. *American Naturalist*, 13:402–404.
- ELLINGER, T. U. H. 1950. *Camarasaurus annae*—A new American sauropod dinosaur. *American Naturalist*, 84: 225–228.
- FRAAS, E. 1908. Ostafrikanische Dinosaurier. *Palaeontographica*, 55:105–144.
- GALTON, P. M. 1984. Cranial anatomy of the prosauropod dinosaur *Plateosaurus*, etc. *Geologia et Palaeontologia*, 18:139–171.
- GILMORE, C. W. 1907. The type of the Jurassic reptile

- Morosaurus agilis* redescribed, with a note on *Campototaurus*. Proceedings of the United States National Museum, 32:151–165.
- . 1920. Osteology of the carnivorous Dinosauria in the United States National Museum. Bulletin of the United States National Museum no. 110, 155 pp., 36 pls.
- . 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. Memoirs of Carnegie Museum, 10:353–367, 5 pl.
- . 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. Memoirs of Carnegie Museum, 11(4):175–300, 15 pl.
- HOLLAND, W. J. 1919. Report on the Section of Paleontology. Annual Report of the Carnegie Museum for 1919:38.
- . 1924. The skull of *Diplodocus*. Memoirs of Carnegie Museum, 9(3):379–403, 4 pl.
- HUENE, F. v. 1914. Über die Zweistämmigkeit der Dinosaurier mit Beiträgen zur Kenntnis einiger Schädel. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, B, 37:577–589.
- . 1926. Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Keuper. Geologische und Paläontologische Abhandlungen, N. F., 19:137–180, pl. 7–13.
- . 1929. Los Saurisquios y Ornithisquios del Cretaceo Argentino. Annales del Museo de La Plata, series 2, 3:1–196, 44 pl.
- . 1932. Die fossile Reptil-Ordnung Saurischia. Monographien zur Geologie und Paläontologie (1), 4, 361 pp.
- JANENSCH, W. 1922. Das Handskelett von *Gigantosaurus brancai* aus den Tendaguru-Schichten Deutsch-Ostafrikas. Centralblatt für Mineralogie, Geologie und Palaeontologie, 1922, pp. 464–480.
- . 1935–1936. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus*, und *Dicraeosaurus* aus dem Tendaguru-Schichten, Deutsch-Ostafrikas. Palaeontographica, Supplement VII; Reihe I, Teil II, pp. 145–308.
- . 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. Palaeontographica, Supplement VII, Reihe 1, Teil 3, pp. 177–235.
- KINGHAM, R. F. 1962. Studies of the sauropod dinosaur *Astrodon* Leidy. Proceedings of the Junior Washington Academy of Sciences, 1:38–44.
- KURZANOV, S. M., AND A. F. BANNIKOV. 1983. New sauropods from the Upper Cretaceous of the Mongolian People's Republic. Paleontological Zhurnal 1983 Nor 2:90–96 (English version).
- LAPPARENT, A. F. DE, AND G. ZBYSZEWSKI. 1957. Les dinosauriens de Portugal. Mémoires Servicos Géologicos Portugal (N.S.) 2, 63 pp.
- LULL, R. S. 1911. Systematic paleontology of the Lower Cretaceous deposits of Maryland, Vertebrata. Maryland Geological Survey—Lower Cretaceous, pp. 183–211, 10 pl.
- MADSEN, J. H., JR. 1976. *Allosaurus fragilis*, a revised osteology. Utah Geological and Mineralogical Survey Bulletin 109, 183 pp., 55 pl.
- MADSEN, J. H., JR., AND W. L. STOKES. 1972. University of Utah cooperative dinosaur project. Proceedings of the Utah Academy of Arts and Letters, 49(1):48–50.
- MANTELL, G. A. 1852. On the structure of the *Iguanodon* and on the fauna and flora of the Wealden Formation. Notices and Proceedings of the Royal Institute of Great Britain, 1:141–146.
- MARSH, O. C. 1877. Notice of new dinosaurian reptiles from the Jurassic formation. American Journal of Science, (3) 14:514–516.
- . 1878a. Notice of new dinosaurian reptiles. American Journal of Science, (3)15:241–244.
- . 1878b. Principal characters of American Jurassic dinosaurs. Part I. American Journal of Science, (3)16: 411–416.
- . 1879. Additional characters of Sauropoda. American Journal of Science, (3)17:86.
- . 1880. Principal characters of American Jurassic dinosaurs, Part III. American Journal of Science, (3)19: 253–259, 6 pl.
- . 1883. Principal characters of American Jurassic dinosaurs, Part VI: Restoration of *Brontosaurus*. American Journal of Science, (3)26:81–85, 1 pl.
- . 1889a. Comparison of the principal forms of Dinosauria of Europe and America. American Journal of Science, (3)37:323–331.
- . 1889b. Notice of new American Dinosauria. American Journal of Science, (3)37:331–336.
- . 1896. Dinosaurs of North America. Sixteenth Annual Report of the United States Geological Survey for 1895, Part I, 414 pp., 85 pl.
- MATEER, N. J., AND J. S. MCINTOSH. 1985. A new reconstruction of the skull of *Euhelopus zdanskyi* (Saurischia: Sauropoda). Bulletin of the Geological Institutions of the University of Uppsala, 11:125–132.
- MCINTOSH, J. S. 1981. Annotated catalogue of the dinosaurs (Reptilia, Archosauria) in the collections of the Carnegie Museum of Natural History. Bulletin of Carnegie Museum of Natural History no. 18, 65 pp., 22 figs.
- . 1990a. Species determination in sauropod dinosaurs with tentative suggestions for their classification. Pp. 53–69, in Dinosaur Systematics (K. Carpenter and P. J. Currie, eds.), Cambridge University Press, Cambridge, England, 318 pp.
- . 1990b. Sauropoda. Pp. 345–401, in The Dinosauria (D. B. Weishampel, P. Dodson, and H. Osmólska, eds.), University of California Press, Berkeley, California, 733 pp.
- MCINTOSH, J. S., AND D. S. BERMAN. 1975. Description of the palate and lower jaw of the sauropod dinosaur *Diplodocus* (Reptilia: Saurischia) with remarks on the nature of the skull of *Apatosaurus*. Journal of Paleontology, 49:187–199.
- NOWINSKI, A. 1971. *Nemegtosaurus mongoliensis*, n. gen., n. sp. (Sauropoda) from the uppermost Cretaceous of Mongolia. Palaeontologia Polonica, 25:57–81.
- OSBORN, H. F. 1903. The skull of *Creosaurus*. Bulletin of the American Museum of Natural History, 19:697–701.
- . 1906. The skeleton of *Brontosaurus* and the skull of *Morosaurus*. Nature, 73:282–284.

- . 1912. Crania of *Tyrannosaurus* and *Allosaurus*. Memoirs of the American Museum of Natural History. I, 1:1–30, 4 pl.
- OSBORN, H. F., AND C. C. MOOK. 1921. *Camarasaurus*, *Amphicoelias*, and other sauropods of Cope. Memoirs of the American Museum of Natural History, n.s., III, 3: 247–387, 26 pl.
- OSTROM, J. H., AND J. S. MCINTOSH. 1966. Marsh's Dinosaurs. Yale University Press, New Haven, Connecticut, 388 pp.
- ROMER, A. S. 1956. The Osteology of the Reptiles. University of Chicago Press, Chicago, Illinois, 772 pp.
- SANZ, J. L., M. L. CASANOVAS, AND J. V. SANTAFÉ. 1987. Dinosaurios del Cretácico inferior de Galve (Teruel, España). Estudios Geológicos Volumen Extraordinario, Galve-Tremp, pp. 45–64.
- SAUVAGE, H. E. 1897/8. Vertébrés Fossiles du Portugal—Contributions à l'étude des Poissons et des Réptiles du Jurassique et du Cretacique. Direction des Travaux Géologique du Portugal, 46 pp.
- WHITE, T. E. 1958. The braincase of *Camarasaurus lentus* (Marsh). Journal of Paleontology, 32:477–493, 5 pl.
- WIMAN, C. 1929. Die Kriede—Dinosaurier aus Shantung. Paleontologia Sinica C, VI, 1, 66 pp.
- ZHANG, Y. 1988. The Middle Jurassic dinosaur fauna from Dashenpu, Zigong, Sichuan. Volume III, Sauropod Dinosaurs, (I) *Shunosaurus*. Sichuan Publishing House of Science and Technology, Chengdu, People's Republic of China, 89 pp. (In Chinese.)

APPENDIX 1

Reported Camarasaurus Skull Materials

Summary of all reported *Camarasaurus* skull materials arranged by locality:

1. *Como Bluff and vicinity, Albany Co., Wyoming.*

A. Marsh Quarry No. 1

YPM 1901, holotype of *Morosaurus grandis*: basioccipital, and basisphenoid.

YPM 1905, paratype of *Morosaurus grandis*: posterior portion of skull consisting of frontals, parietals, postorbitals, squamosals, quadrates, quadratojugals, pterygoids, left ectopterygoid, supraoccipital, exoccipitals, opisthotics, prootics, laterosphenoids, orbitosphenoids, basioccipital, basisphenoid, disarticulated maxillae (incomplete), and dentary.

B. Marsh Quarry No. 3

YPM 1907: There are three partial skulls from Quarry 3 catalogued YPM 1907 and 1912. YPM 1907 includes two skulls, one larger than the other, with many elements incomplete due to poor collecting. Elements of the two skulls are not fully separated and include: premaxillae, maxillae, left frontal and parietal, postorbitals, quadrates (fragmentary), pterygoids (fragmentary), ectopterygoid, supraoccipital, exoccipitals, opisthotics, right prootic, right laterosphenoid, basioccipital, basisphenoid, parasphenoid, dentary (fragmentary), angulars, prearticulars (fragmentary), and left articular.

YPM 1912: frontals, parietals, postorbital, right squamosal, quadrates (fragmentary), pterygoid, right exoccipital and opisthotic, left ectopterygoid, and fragment of palatine.

C. Marsh Quarry No. 8

YPM 4844: two teeth.

D. Marsh Quarry No. 9

YPM 4194: tooth.

E. Marsh Quarry No. 12

YPM 4766: two teeth.

YPM 4768: two teeth.

F. Marsh Quarry No. 13

YPM 1910, holotype of *Camarasaurus lentus*: left premaxilla, maxillae, and left dentary and quadrate (fragmentary).

USNM 7759, right premaxilla.

USNM 7944 1: maxilla; supraoccipital (incomplete), right exoccipital, right opisthotic, occipital condyle, and right dentary (incomplete) not numbered but probably belonging to the same skull.

2. *Other localities in southeastern Wyoming.*

A. Bone Cabin Quarry northeast of Medicine Bow, Wyoming

AMNH 467: greater part of skull consisting of maxillae, premaxillae, nasals, jugals, frontal, right postorbital, left quadratojugal (incomplete), pterygoids, ectoptery-

goid, part of braincase, and mandibles.

AMNH 607: right dentary.

AMNH 611: right maxilla.

AMNH 618: both maxillae.

AMNH 657: left dentary.

AMNH 673: cranium.

AMNH 677: right premaxilla.

AMNH 6126: cranium.

B. Sheep Creek (Quarry C), Wyoming

CM 113: left maxilla, left postorbital, and right dentary.

C. Red Fork of the Powder River, Wyoming

CM 312: left dentary.

3. *Colorado*.

A. Garden Park, Colorado—Cope Quarry 2

AMNH 5761: left maxilla, right quadrate, right pterygoid (incomplete), left parietal articulated with braincase consisting of supraoccipital, exoccipitals, opisthotics, prootics, laterosphenoids, basioccipital, basisphenoid, and two right dentaries.

B. Webster Park, Colorado

YPM 619: left premaxilla, left maxilla, complete braincase, and right dentary.

4. *Utah*.

A. Dinosaur National Monument, north of Jensen, Utah

CM 11338: complete, articulated skull and mandibles, including stapes and hyoid elements.

USNM 13786 (formerly CM 11373): articulated skull and mandibles somewhat crushed, but essentially complete except for badly damaged left nasal and posterior half of right mandible. The palate, braincase, and much of the medial surface of the mandibles are still covered by matrix.

DNM 28: greater part of a disarticulated skull and mandibles lacking the left lacrimal, palatines, vomers, and all medial elements of the mandibles except the left prearticular.

CM 11969: disarticulated skull only partially worked out consisting of the complete braincase, both postorbitals, both maxillae, left premaxilla, one pterygoid, both dentaries, both surangulars, right prearticular, and other elements not yet prepared.

DNM 975: the "cliff skull" has been left in place on the quarry face, with the right side prepared in relief. All the external elements of the right side are articulated except the quadratojugal, which has been displaced ventrally, and the quadrate, which has not been found. The posterior and dorsal surfaces of the skull are exposed, showing the supraoccipital, exoccipitals, opisthotics, basioccipital, left quadrate, left quadratojugal, parietals, frontals, and nasals, in position. Many bones of the palate are missing, and those present have been more or less displaced. The right pterygoid and ectopterygoid have been displaced ventrally over the medial surface of the left mandible. The left pterygoid and right palatine have been removed and prepared. The articulated dentary, angular, and surangular of the right mandible, as well as the disarticulated right prearticular, angular, and splenial have also been removed from the quarry and fully prepared.

CM 12020: imperfect skull with mandibles (belongs to CM 11393).

CM 21751: right premaxilla, and lateral elements of both mandibles.

CM 21732: parts of a poorly preserved skull consisting of the right maxilla, left quadratojugal, left quadrate, right dentary, and fragments.

CM 21702: left maxilla.

CM 3381: large tooth, probably premaxillary.

DNM 1009: probably includes the greater part of the skull that is exposed on the quarry face and referred to as the "hump skull." Some elements displaced by compression against lower end of a right sauropod femur and possibly lost. Exposed elements include the left articular, left prearticular, left angular, left surangular, left quadrate, left pterygoid, left ectopterygoid, right squamosal, right opisthotic, right prootic, right laterosphenoid, right pterygoid, supraoccipital, and right parietal.

DNM 32-37: teeth.

- DNM 948–951, 953–971: teeth.
DNM 4011: right dentary.
DNM 3008: partial, articulated skull questionably belonging to *Camarasaurus* consisting of right prefrontal, frontals, parietals, postorbitals, squamosals, laterosphenoids, prootics, opisthotics, exoccipitals, and supraoccipital.
DNM 3699: right premaxilla.
DNM 4257: right maxilla.
BYU Carnegie Museum field no. 320/C given to BYU: right maxilla
- B. Jensen Quarry, near Dinosaur National Monument, Jensen, Utah
BYU 9048: complete braincase and portions of upper and lower jaws.
- C. Cleveland-Lloyd Dinosaur Quarry east of Cleveland, Emery County, Utah
UUVP 4008 (l), 1223 (r), 3999 (r), 3859 (l), 5645 (r), 10062 (l): premaxillae.
UUVP 1859 (l), 3954 (l), 1860 (r), 4005 (r): maxillae.
UUVP 5644 (l), 5108 (l), 3963 (r): nasals.
UUVP 3371 (r): lacrimal.
UUVP 5126 (r), 5036 (l), 3568 (l): prefrontals.
UUVP 3293 (l), 10063 (l): quadratojugal.
UUVP 3359 (l), 2300 (r), 5434 (r): postorbitals.
UUVP 1984 (l), 1985 (l), 2625 (l), 3638a (l), 5679 (l), 5643 (r): quadrates.
UUVP 3507 (l), 5806 (l), 4020 (r), 10064 (p): squamosals.
UUVP 3350 (l), 1986 (r), 3369 (r), 4309 (l), 5259 (l), 10071 (l), 10795 (r): pterygoids.
UUVP 4270 (l), 5115 (l), 5593 (r): ectopterygoids.
UUVP 5065 (r): vomer.
- UUVP 3568: *Camarasaurus*-like skull *b* that includes left prefrontal, frontals, and parietals articulated with braincase consisting of supraoccipital, exoccipitals, orbitosphenoids, laterosphenoids, prootics, exoccipital, opisthotic, basioccipital, and basisphenoid (incomplete), and associated lacrimal UUVP 3371.
UUVP 10070: complete braincase articulated with right lacrimal; UUVP 10062–10072 are associated as a partial skull.
UUVP 4286: complete braincase.
UUVP 10795: articulated left prefrontal and frontal, parietals articulated with braincase consisting of supraoccipital, exoccipitals, opisthotics, prootics, laterosphenoids, orbitosphenoids, basioccipital, and basisphenoid–parasphenoid, and associated right lacrimal, left squamosal, right quadrate, right pterygoid, and right surangular, left jugal, and postorbitals. This specimen is referred to as *Camarasaurus*-like skull *a*.
UUVP 5684: braincase consisting of weathered basioccipital, exoccipitals, basioccipital (incomplete), and supraoccipital (incomplete).
UUVP 3887, 4323: jaw fragments.
UUVP 3609 (l), 1529 (r), 2655 (r), 3610 (r): dentaries.
UUVP 4027 (l), 3221 (r), 6820 (r), 10065 (l): surangular.
UUVP 10068 (l): angular.
UUVP 4939 (l): articular.
UUVP 5073 (l): prearticular.
UUVP 1937–1973: teeth.
BYU 11626 (l): dentary.

APPENDIX 2

Abbreviations for Figures

The following abbreviations are used in figures, with some identifying not only individual bones but also their areas of contact on bones with which they articulate:

amf, anterior maxillary foramen	pa, palatine
a, angular	pf, postfrontal
aof, antorbital fenestra	pl, pleurocoel
ar, articular	pm, premaxilla
bo, basioccipital	pmp, premaxillary process
bp, basipterygoid process	pp, parapophysis
bs, basisphenoid	po, postorbital
c, coronoid	pop, paroccipital process
d, dentary	poz, postzygapophysis
dmp, dorsal maxillary process	pr, prootic
ec, ectopterygoid	pra, prearticular
en, external naris	prf, prefrontal
eo, exoccipital	prz, prezygapophysis
f, frontal	ps, parasphenoid
fm, foramen magnum	pt, pterygoid
ic, intercoronoid	ptf, posttemporal fenestra
in, internal naris	q, quadrate
itf, infratemporal fenestra	qj, quadratojugal
j, jugal	qjp, quadratojugal process
l, lacrimal	sa, surangular
lf, lacrimal foramen	saf, surangular foramen
lp, lacrimal process	snf, subnarial foramen
ls, laterosphenoid	so, supraoccipital
m, maxilla	sp, splenial
n, nasal	sq, squamosal
np, nasal process	st, stapes
o, orbit	stf, supratemporal fenestra
od, odontoid	suf, subtemporal fenestra
op, opisthotic	tr, transverse process
os, orbitosphenoid	v, vomer
p, parietal	vmp, ventral maxillary process

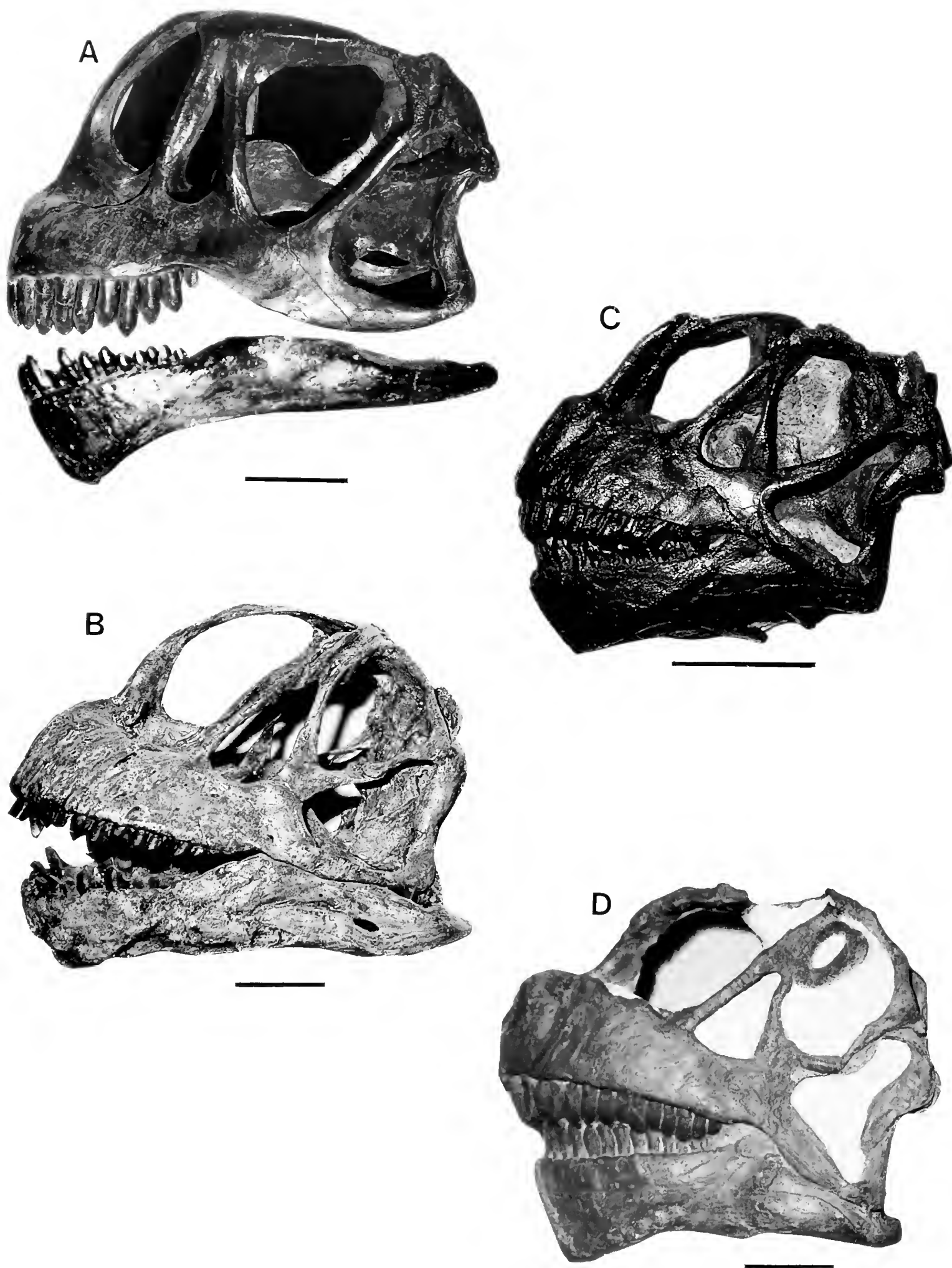


Fig. 1.—*Camarasaurus* skulls in lateral view. A, *C. grandis*, paratype, YPM 1905, partially restored; B, *C. lentus* DNM 28 (cast); C, *C. lentus* CM 11338; D, *C. lentus* DNM 13786; E, *C. ?grandis* AMNH 467, drawing of reconstructed, badly crushed skull (after Osborn, 1906); and F, *C. lentus* DNM 975 ("cliff skull"). Scales = 10 cm.

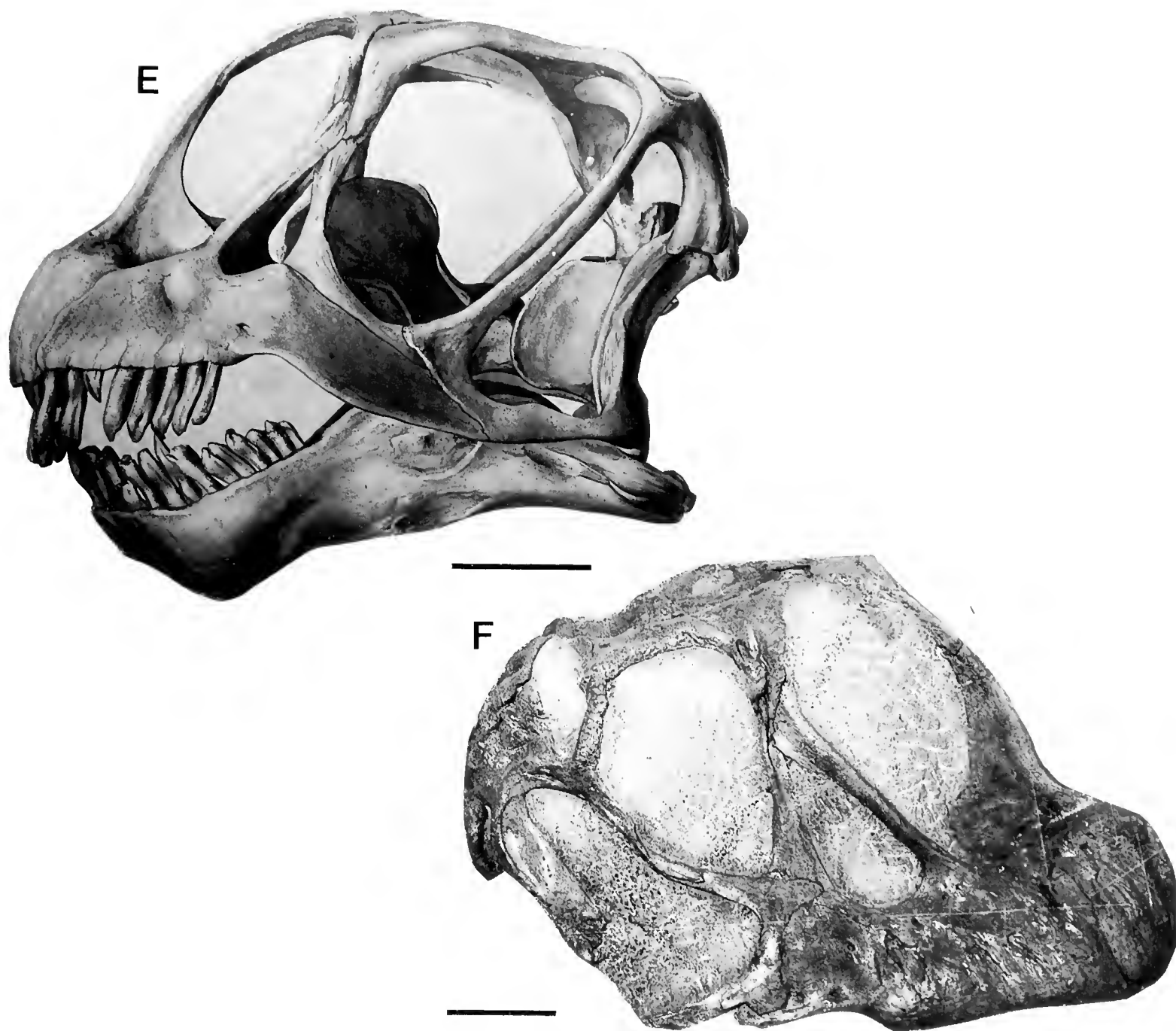


Fig. 1.—*Continued*.

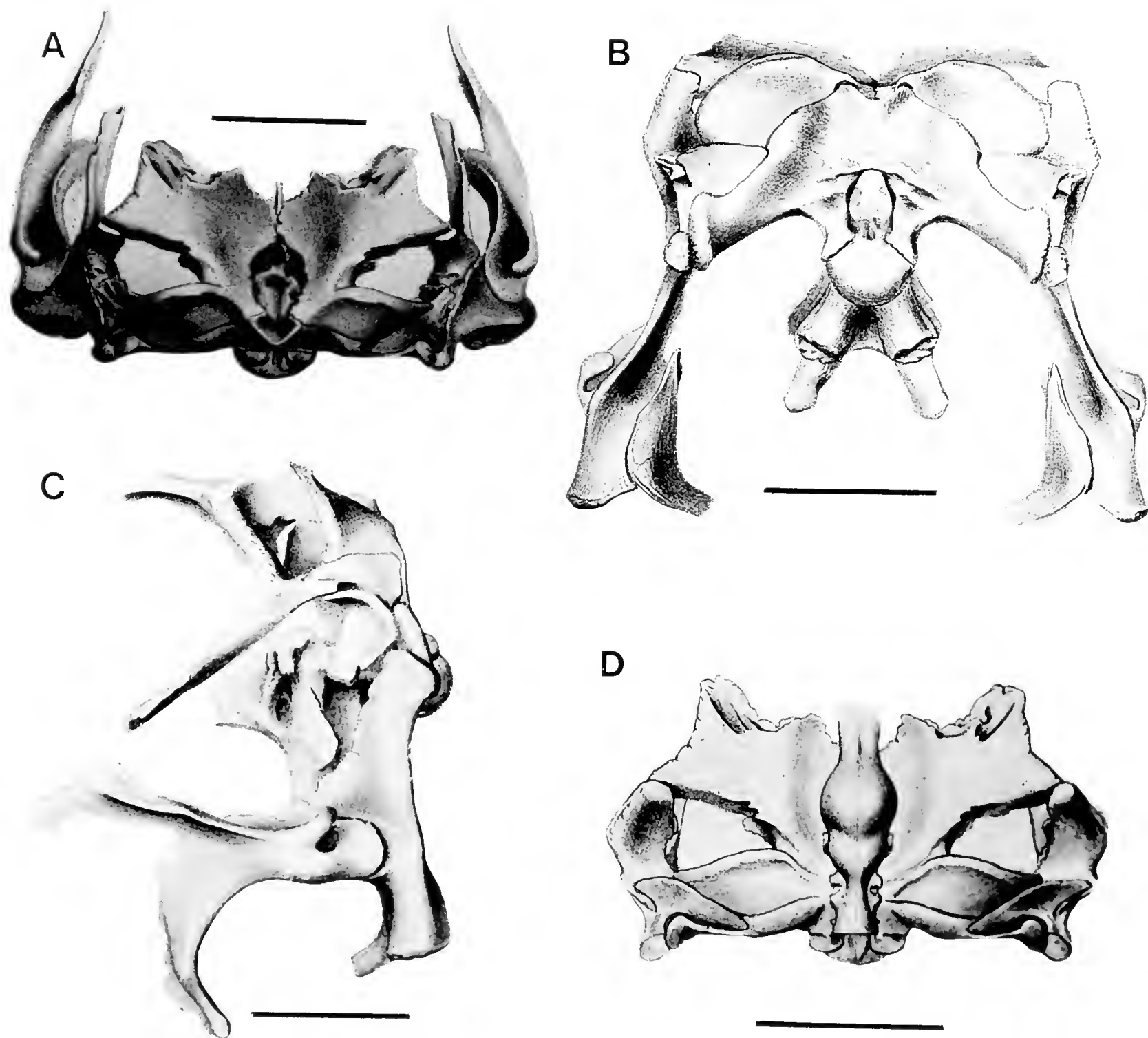


Fig. 2.—Occipital regions of skulls of *Camarasaurus*. A, dorsal; B, posterior; and C, left lateral views of *C. grandis*, paratype, YPM 1905, are unpublished illustrations prepared under the direction of Marsh in which the quadrate and pterygoid are incorrectly positioned; D, E, corrected versions of A and B published by Marsh (1896); and F, posterior view of *C. supremus* AMNH 5761 (after Osborn and Mook, 1921). Scales = 10 cm.

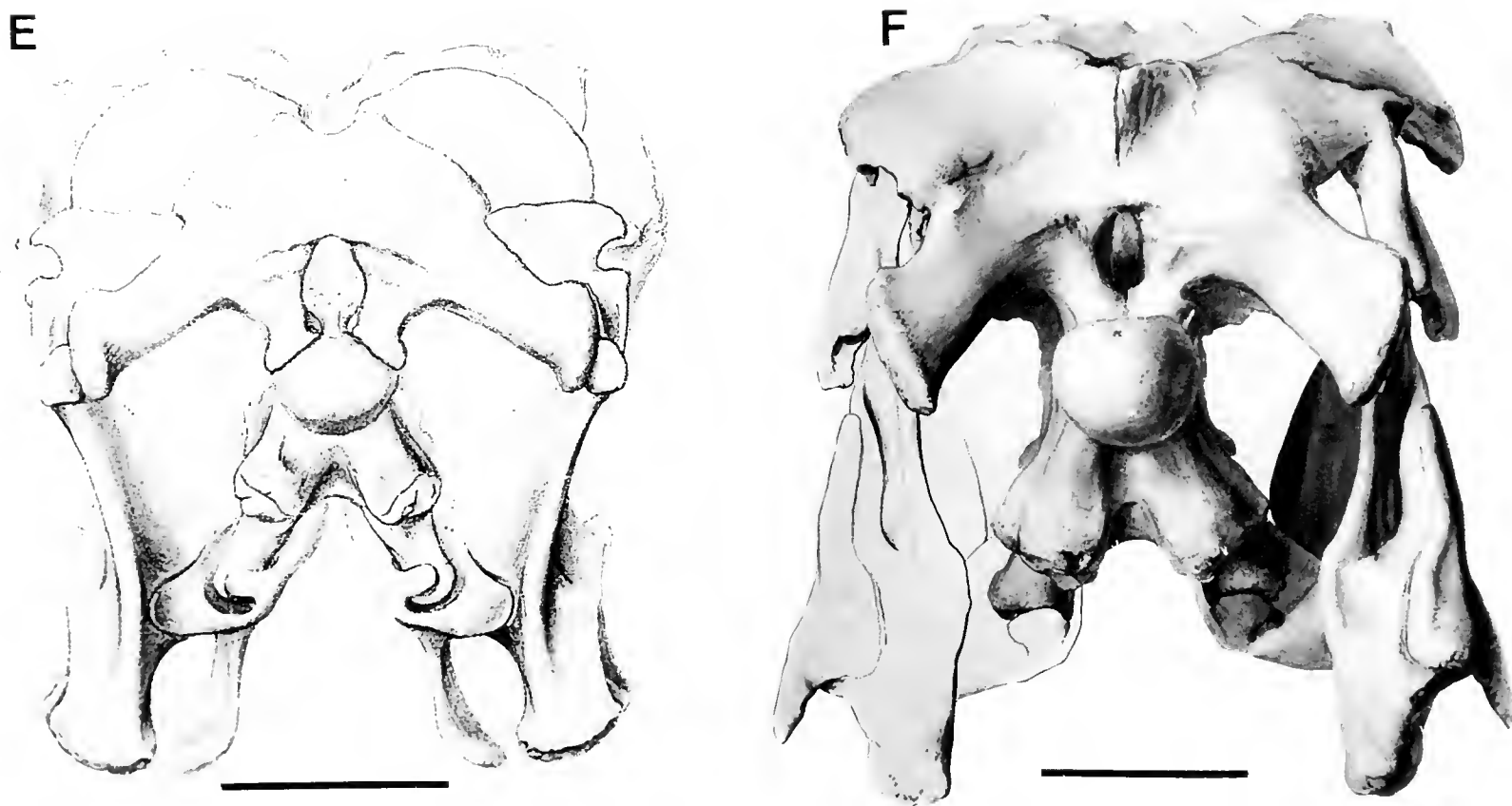


Fig. 2.—*Continued.*

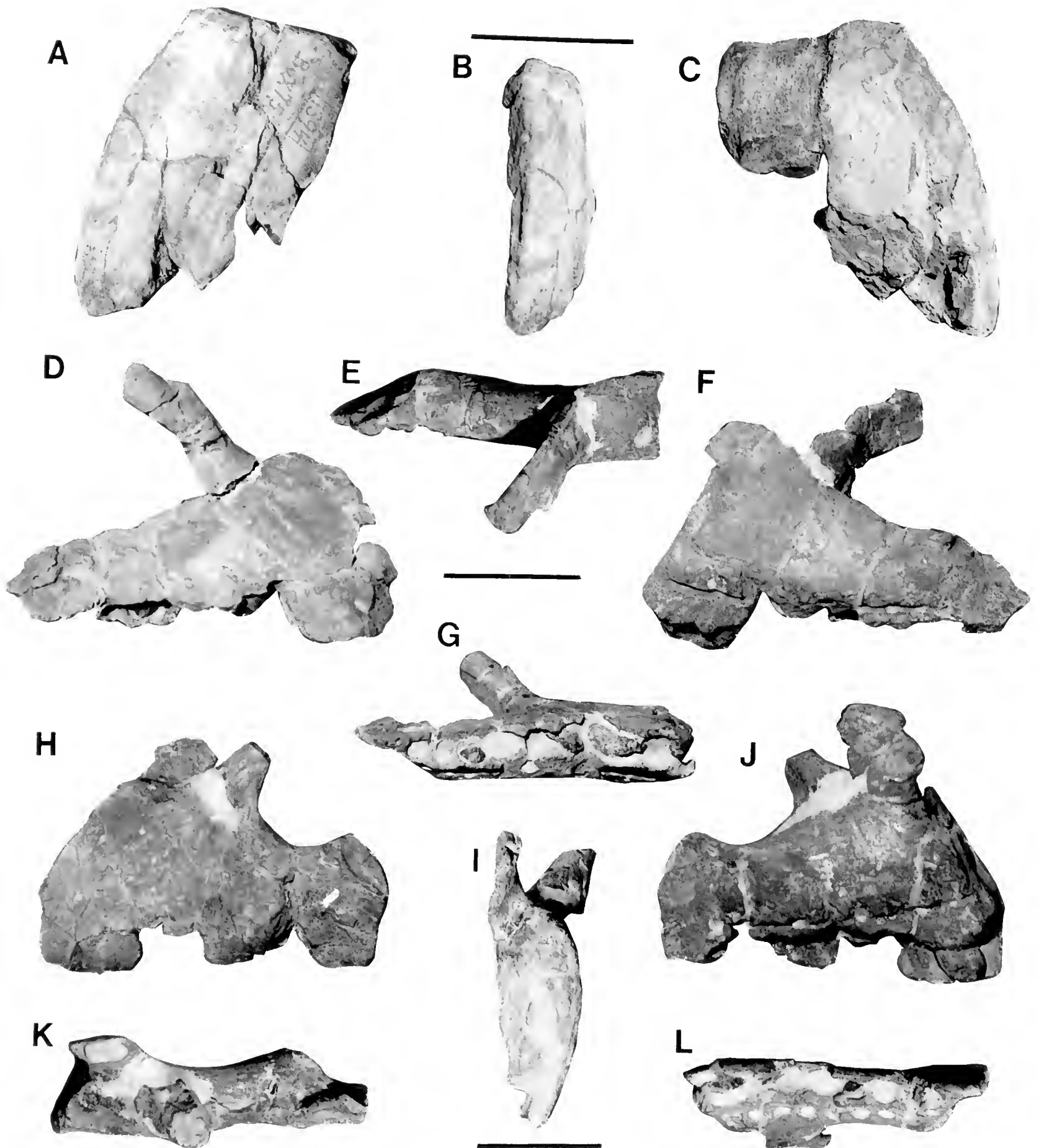


Fig. 3.—Disarticulated, incomplete elements of skull and mandible of *Camarasaurus lentus*, holotype, YPM 1910. A, lateral; B, anterior; and C, medial views of left premaxilla. D, lateral; E, dorsal; F, medial; and G, ventral views of right maxilla. H, lateral; I, anterior; J, medial; K, dorsal; and L, ventral views of left maxilla. M, dorsal; N, lateral; O, posterior; and P, ventral views of basioccipital. Q, lateral; R, anterior; S, medial; and T, posterior views of distal end of left quadrate. U, lateral; and V, medial views of left dentary. Scales = 5 cm.

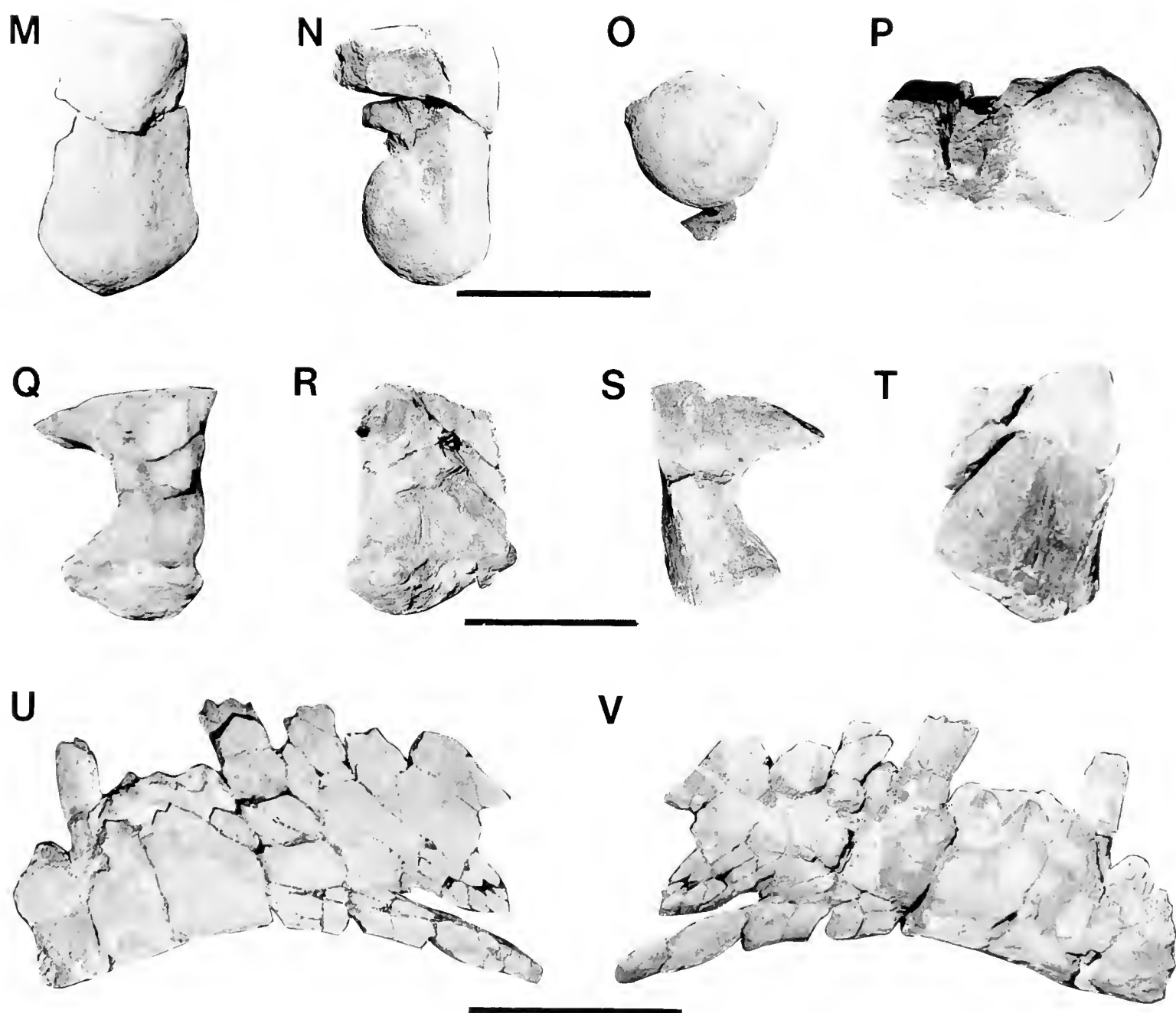


Fig. 3.—Continued.

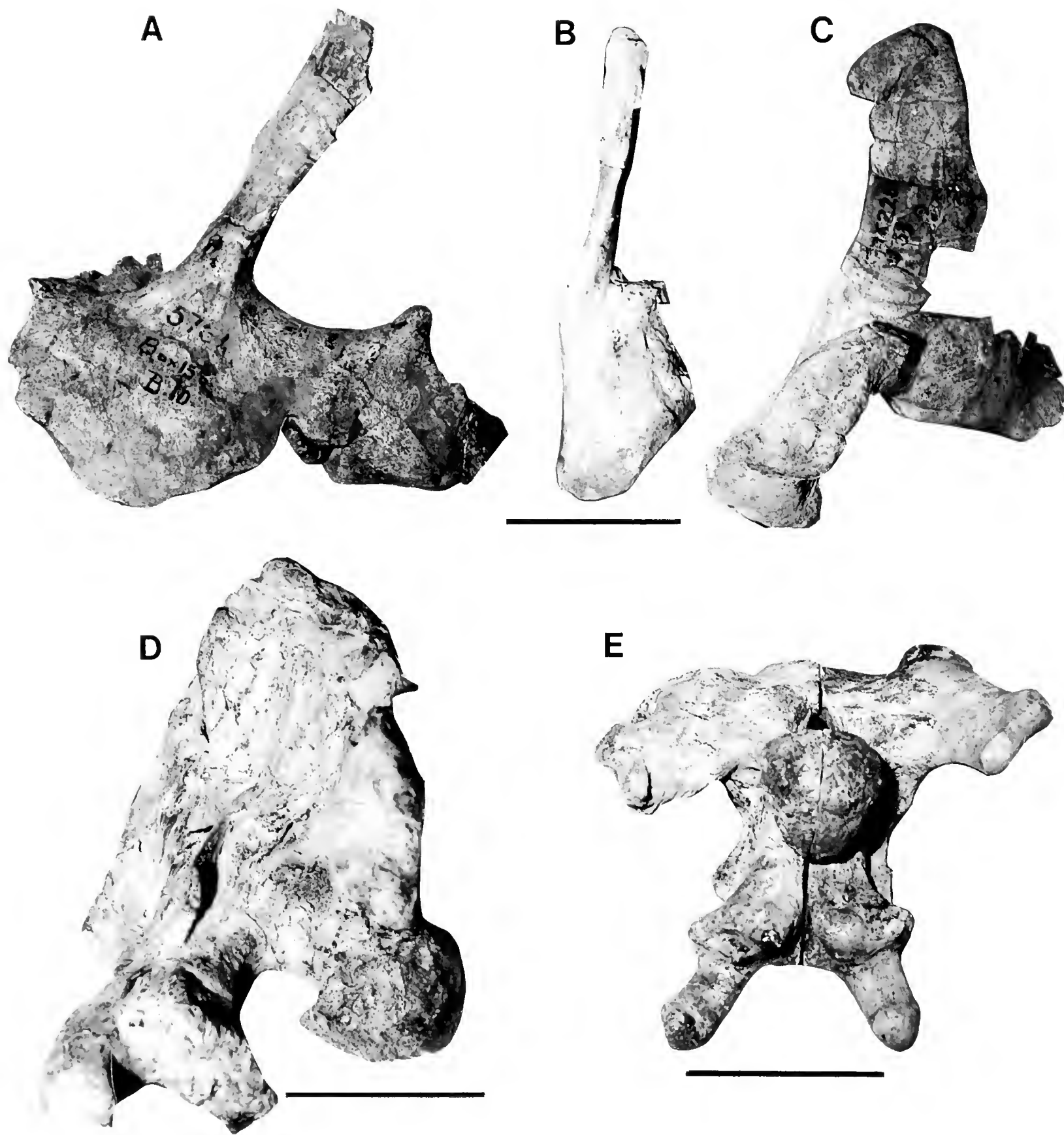


Fig. 4.—Disarticulated elements of skull and mandible of *Camarasaurus supremus* AMNH 5761. A, lateral view of left maxilla; B, posterior view of right quadrate; C, lateral view of right quadrate with fragment of pterygoid attached; D, E, lateral and posterior views, respectively, of braincase; F, lateral view of right dentary; and G, lateral view of second right dentary included in AMNH 5761. Scales = 10 cm.

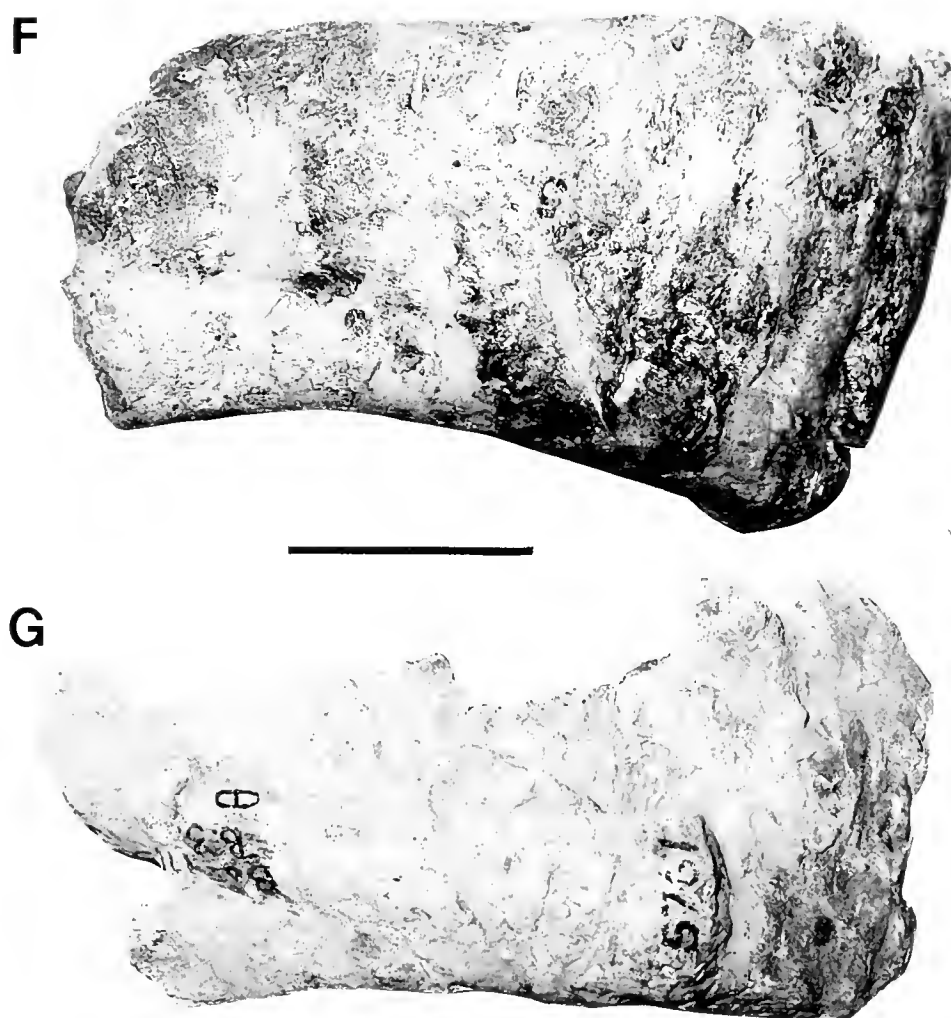


Fig. 4.—*Continued.*

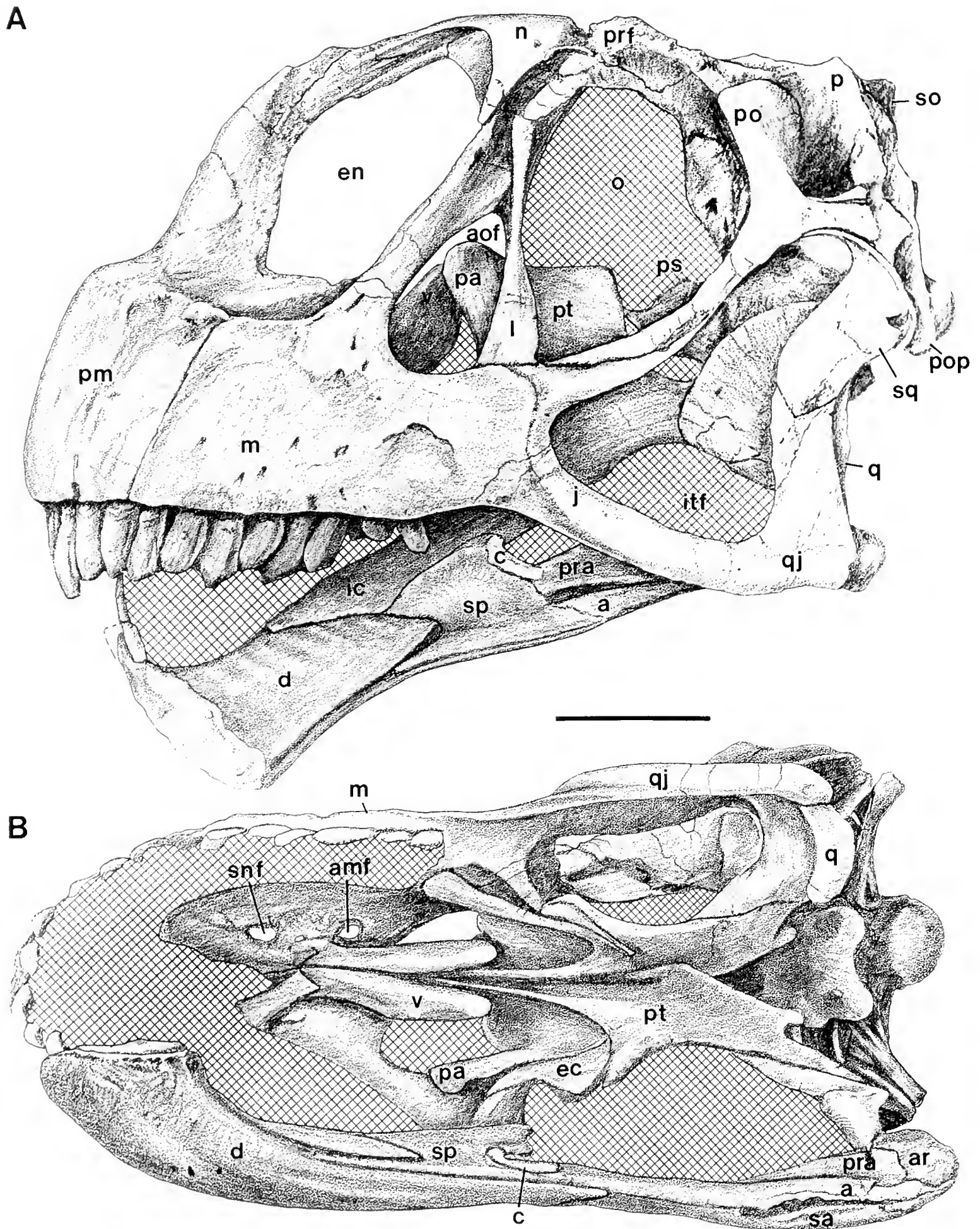


Fig. 5.—Skull of *Camarasaurus lentus* CM 11338 with left mandibular ramus removed. A, left lateral; B, palatal; C, dorsal; D, anterior; and E, occipital views. Scales = 5 cm.

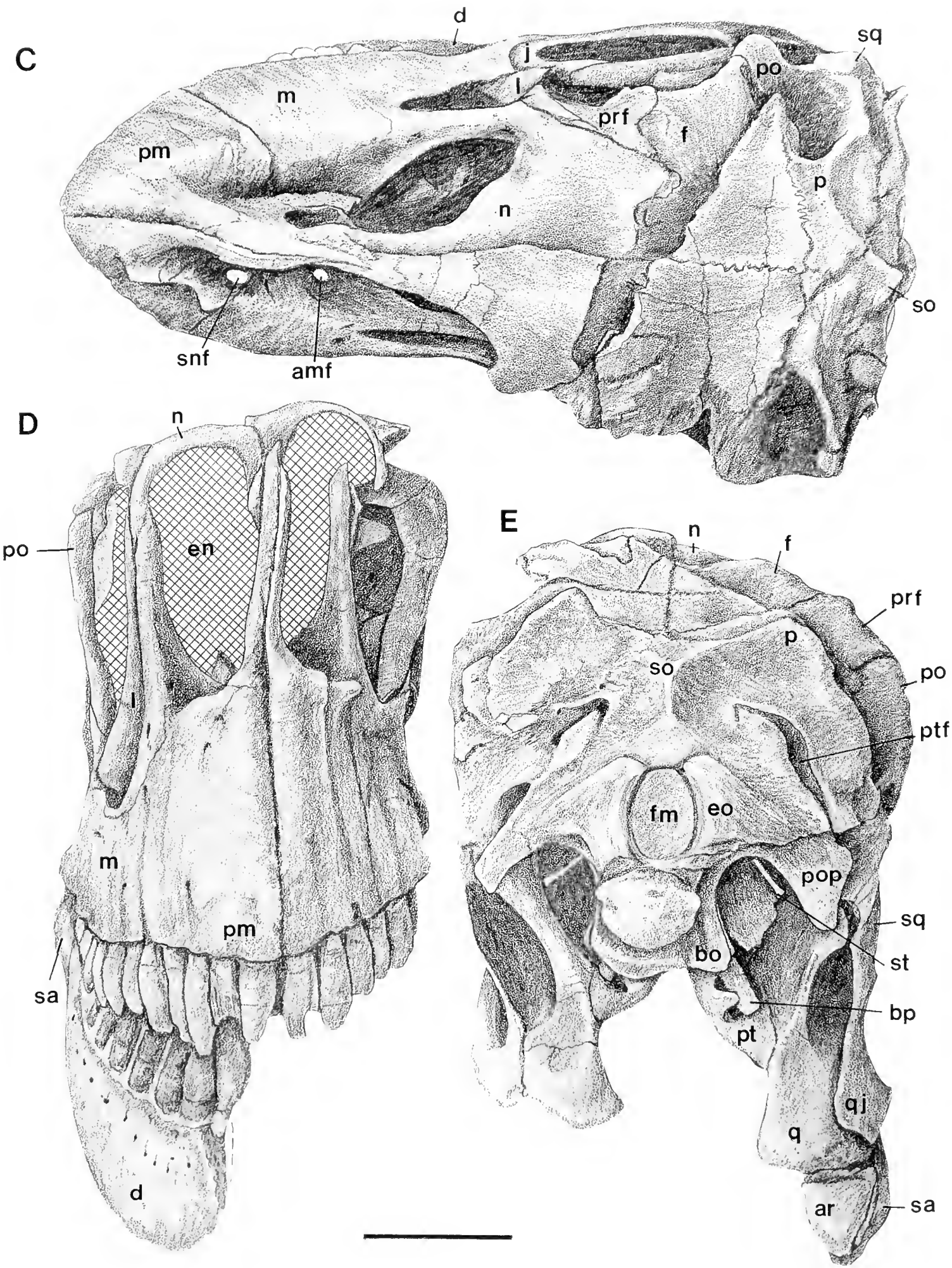
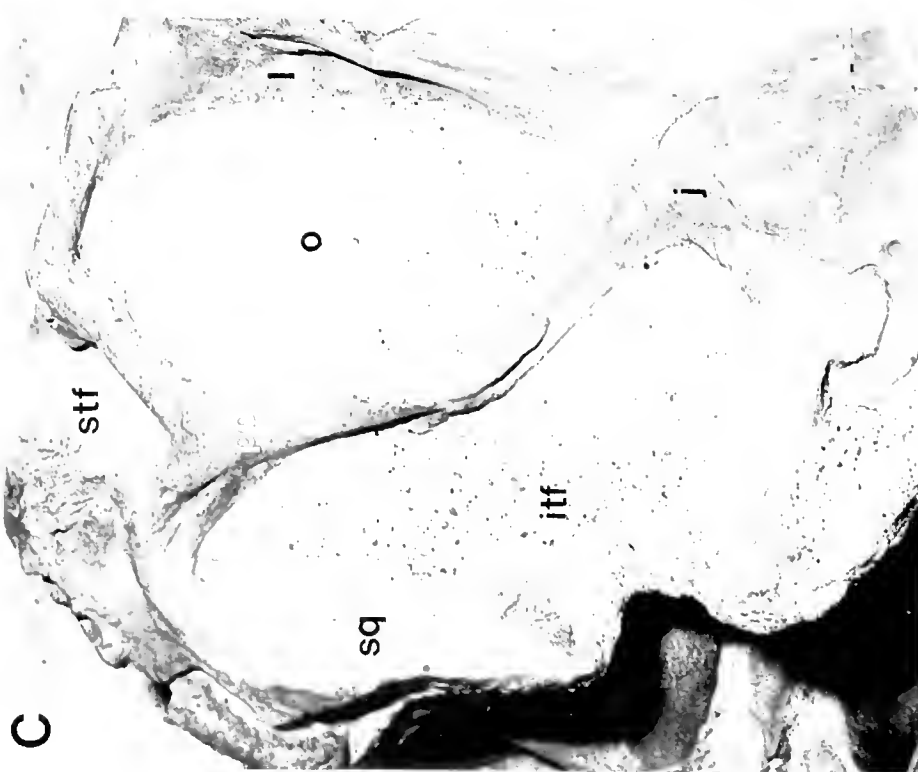
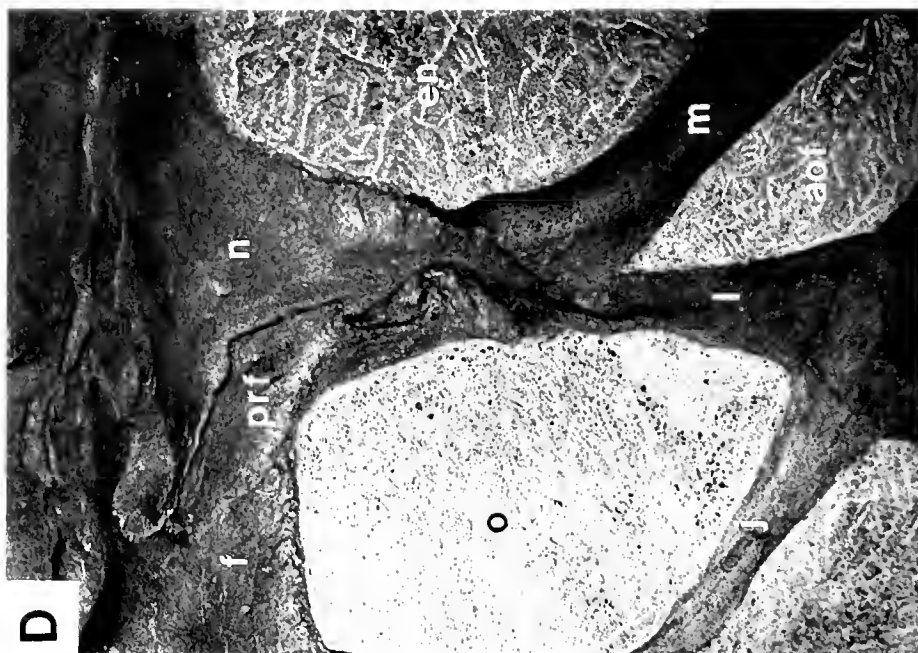
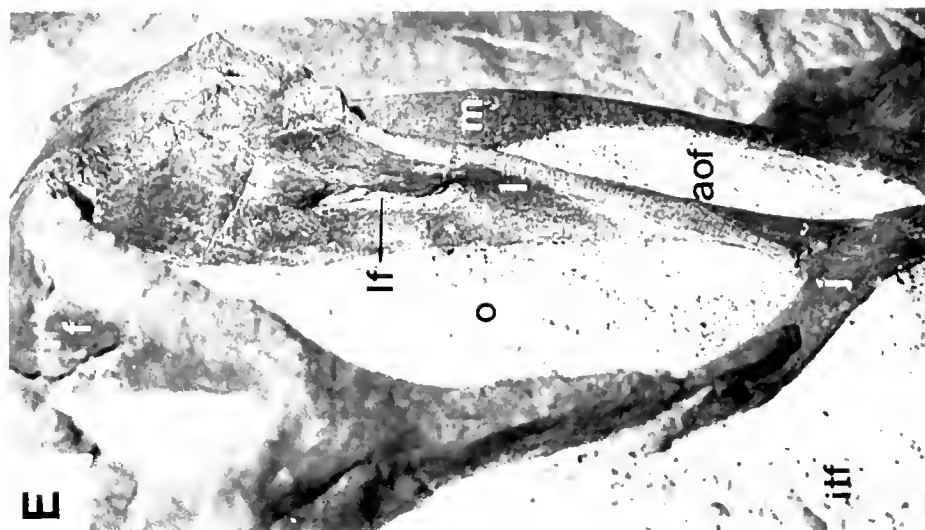
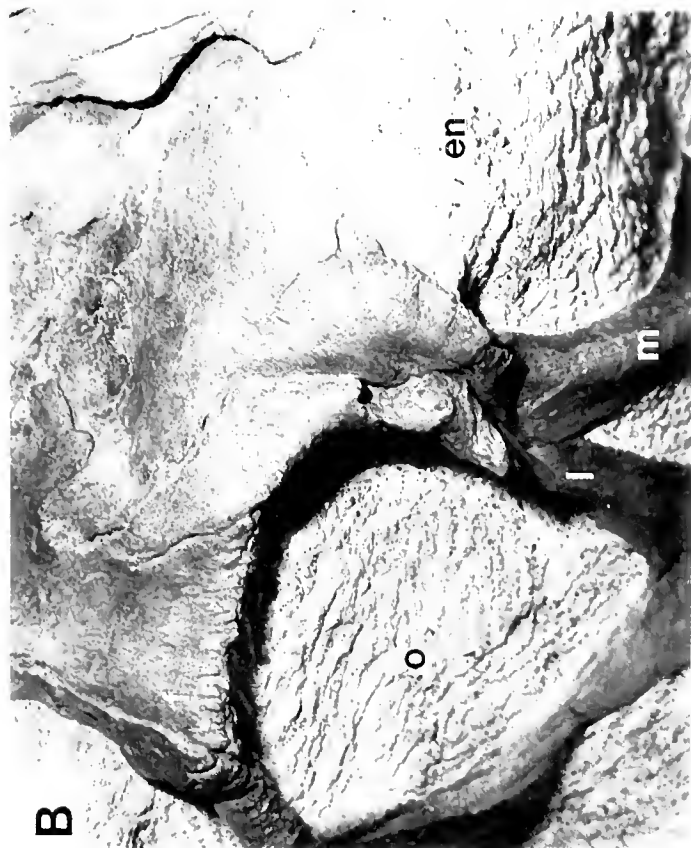


Fig. 5.—Continued.

Fig. 6.—*Camarasaurus lentus* DNM 975 (“cliff skull”), showing various views of the right, posterior region of the skull roof to illustrate structural details. A, dorsolateral view showing sutures between postorbital, parietal, and frontal; B, dorsolateral, slightly anterior view showing sutures between frontal, prefrontal, and nasal; C, lateral view showing sutures between squamosal, postorbital, and jugal (quadrate and quadratojugal removed). Note the overlapping jugal–maxilla contact and the slender posteriorly projecting process of the jugal which are otherwise partially hidden by the quadratojugal; D, dorsolateral view showing complex sutures between prefrontal, nasal, lacrimal, and maxilla; and E, posterior view showing the lacrimal foramen. →



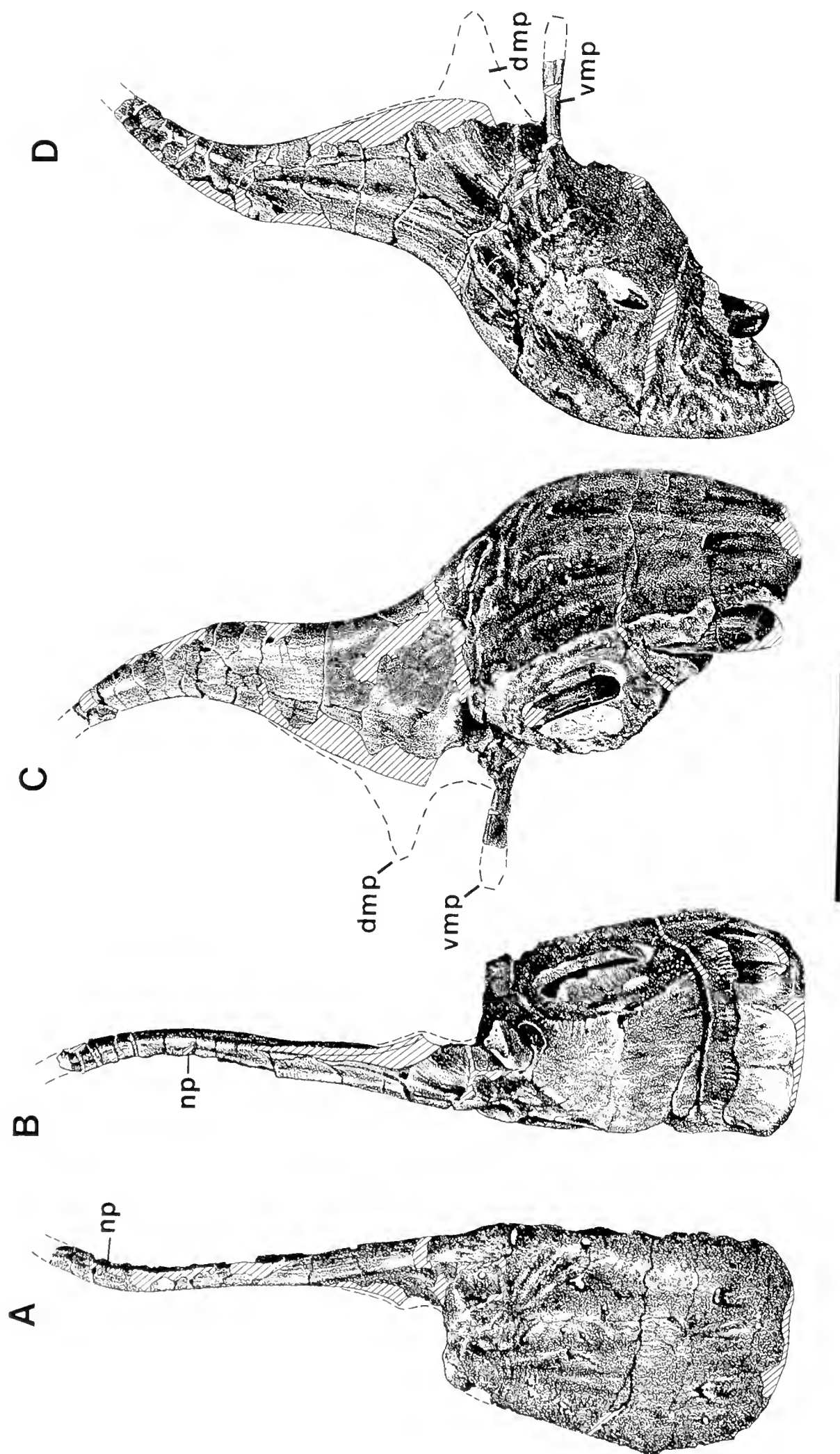


Fig. 7.—Premaxillae of *Camarasaurus* sp. A–D, UUVP 3999 (r); E–H, UUVP 10062 (l); and I–L, UUVP 5645 (r). A, E, I, anterior; B, F, J, posterior; C, G, K, lateral; and D, C, L, medial views. Scales = 10 cm.

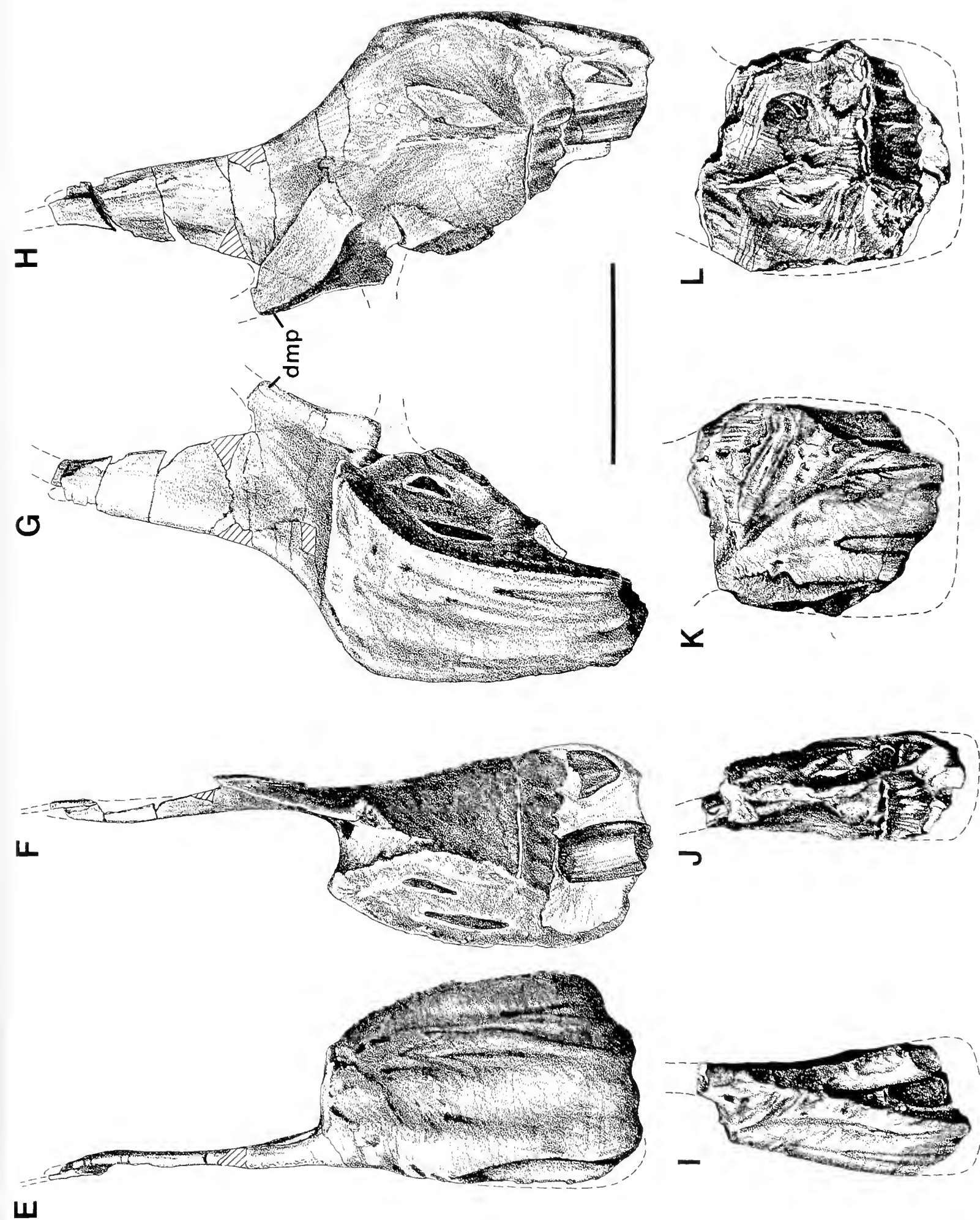
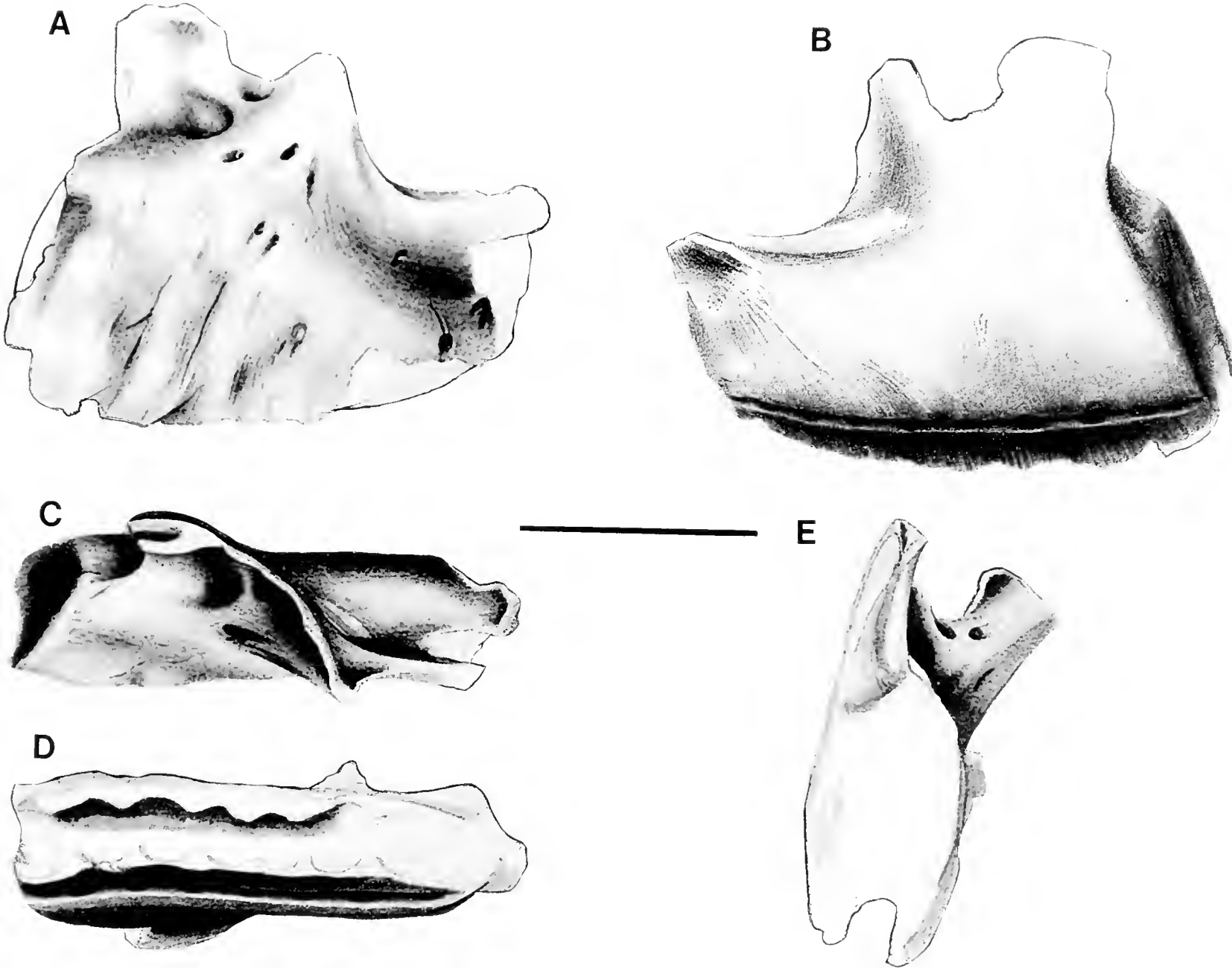


Fig. 7.—Continued.

Fig. 8.—Left maxilla of *Camarasaurus grandis*, paratype, YPM 1905. A, lateral; B, medial; C, dorsal; D, ventral; and E, anterior views. Unpublished drawings prepared under the direction of Marsh. Scale = 10 cm. →



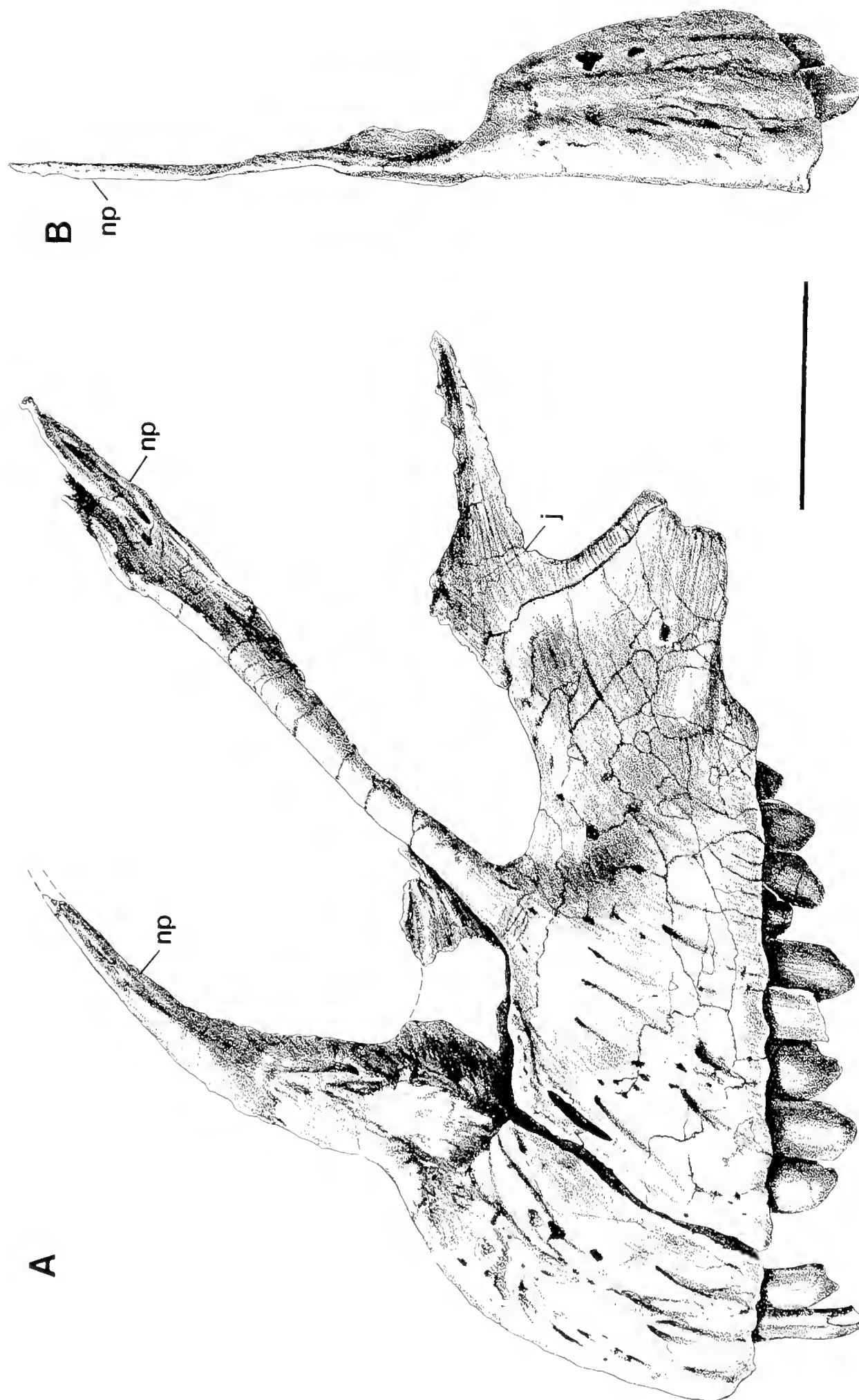


Fig. 9.—*Camarasaurus lentus* DNM 28. A, C, lateral and medial views, respectively, of articulated left premaxilla, maxilla, and jugal; B, D, anterior and posterior views, respectively, of left premaxilla; and E, dorsal view of articulated left maxilla and jugal. Scales = 10 cm.

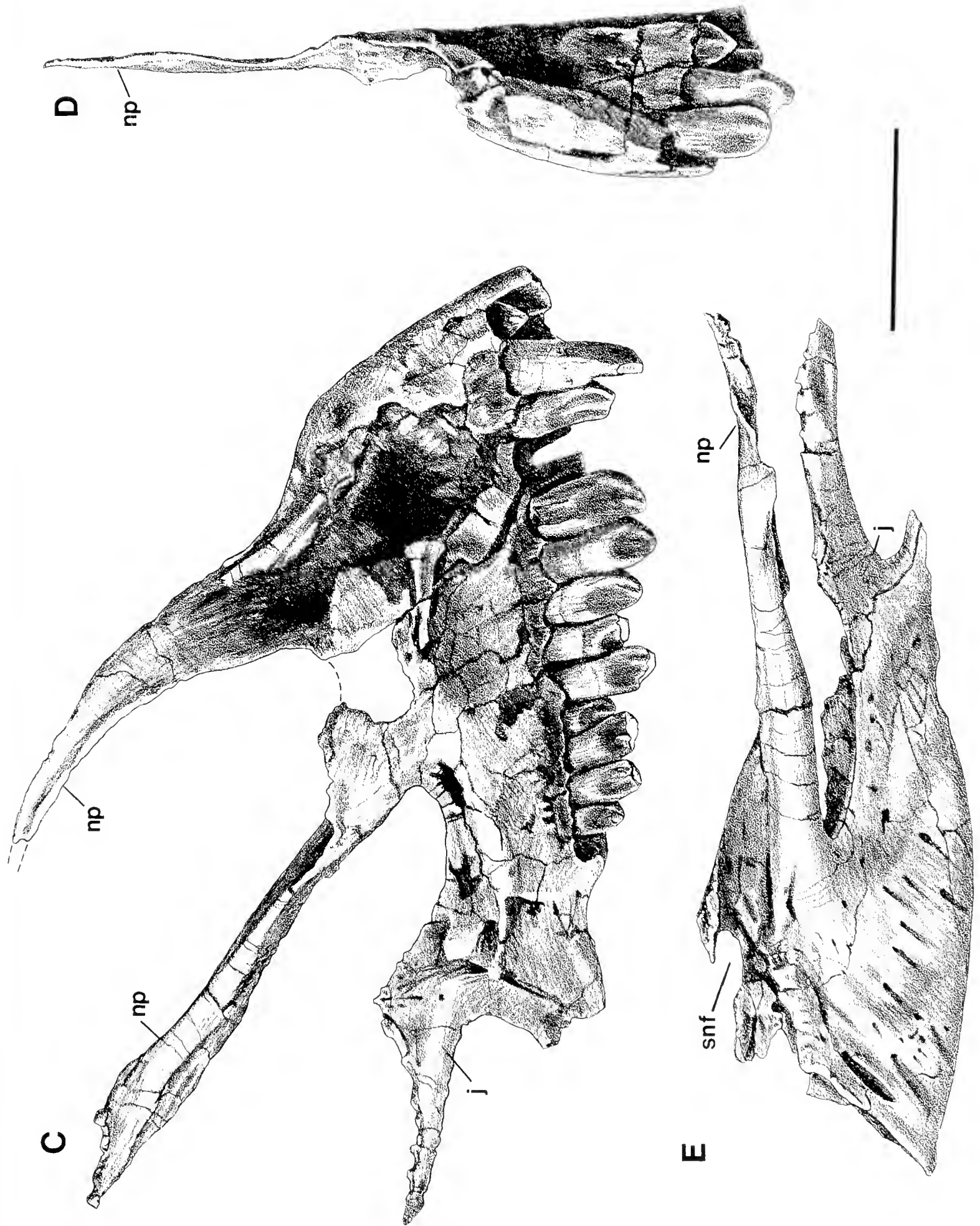
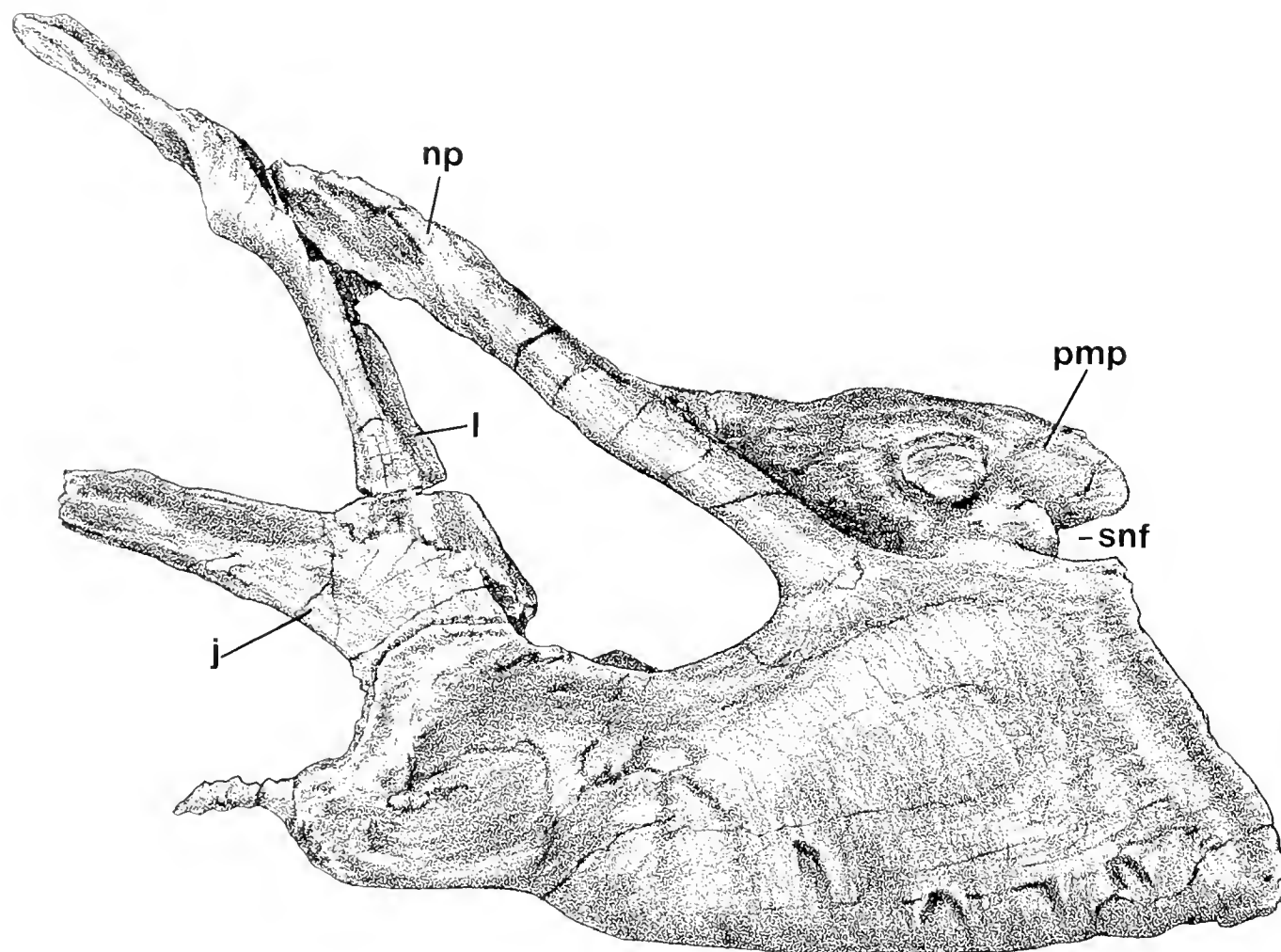


Fig. 9.—Continued.

A



B

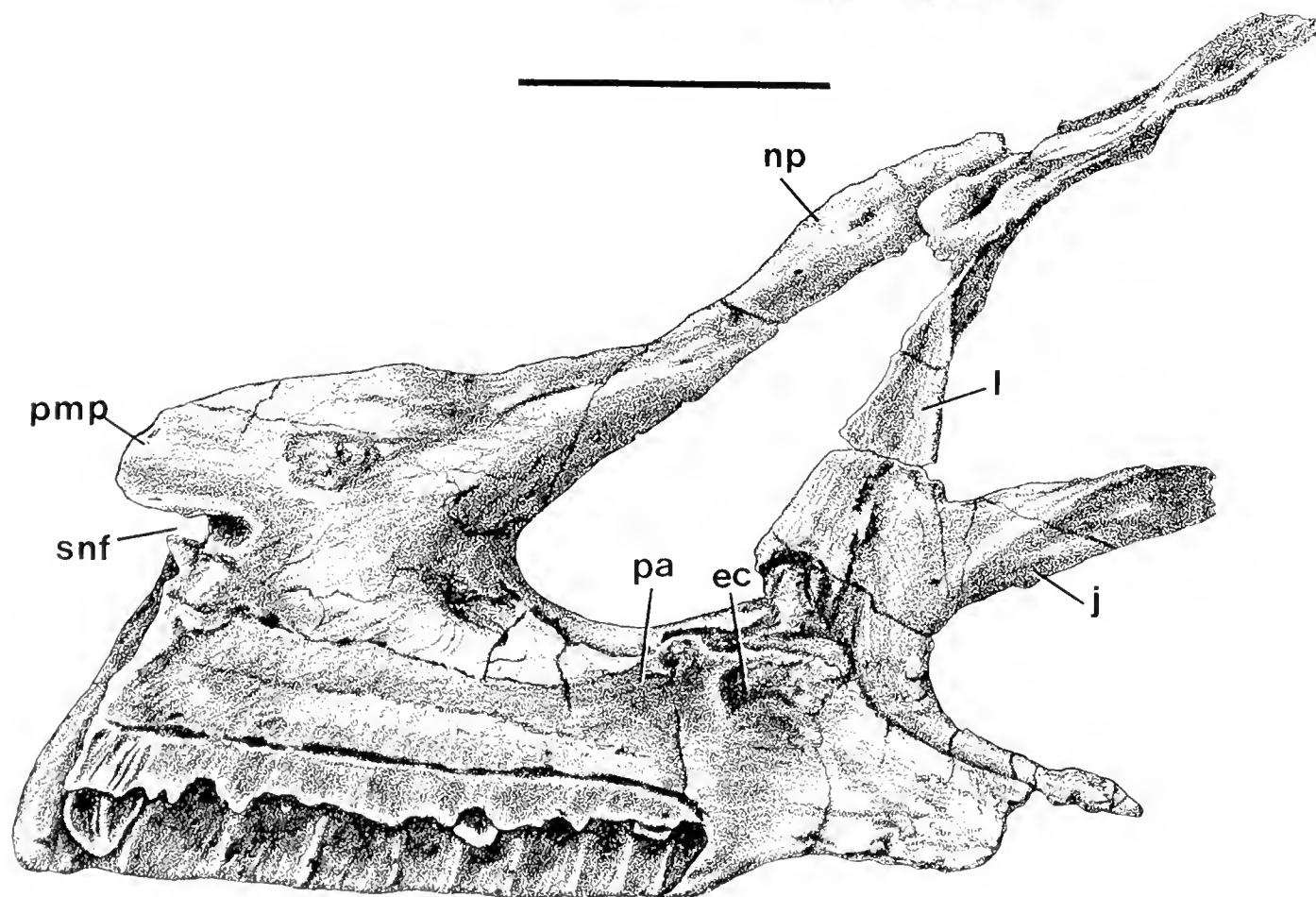


Fig. 10.—Articulated right maxilla, lacrimal, and jugal of *Camarasaurus lentus* DNM 28. A, lateral; and B, medial views. Scale = 10 cm.

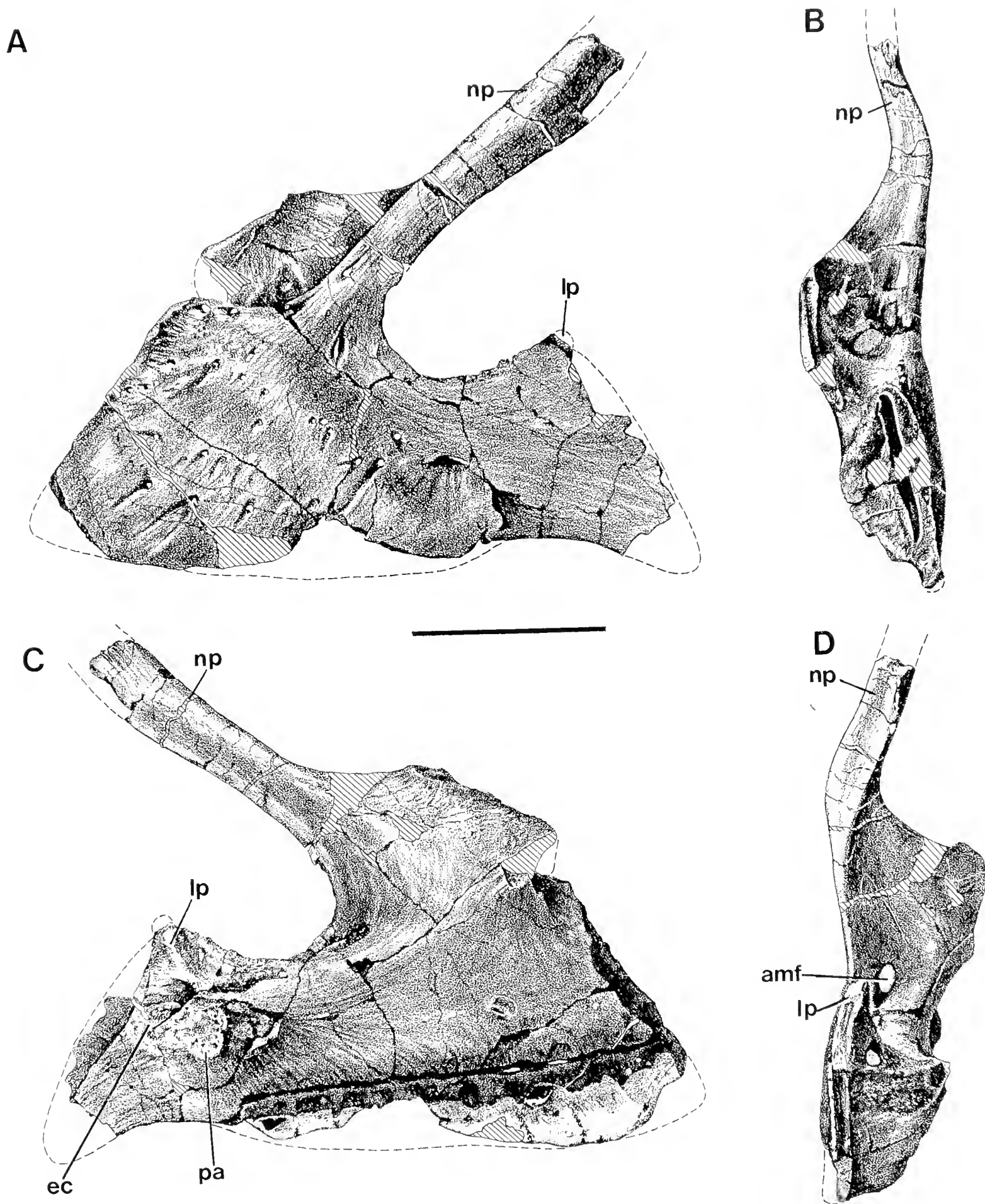


Fig. 11.—Left maxilla of *Camarasaurus* sp. UUVP 1859. A, lateral; B, anterior; C, medial; and D, posterior views. Scale = 10 cm.

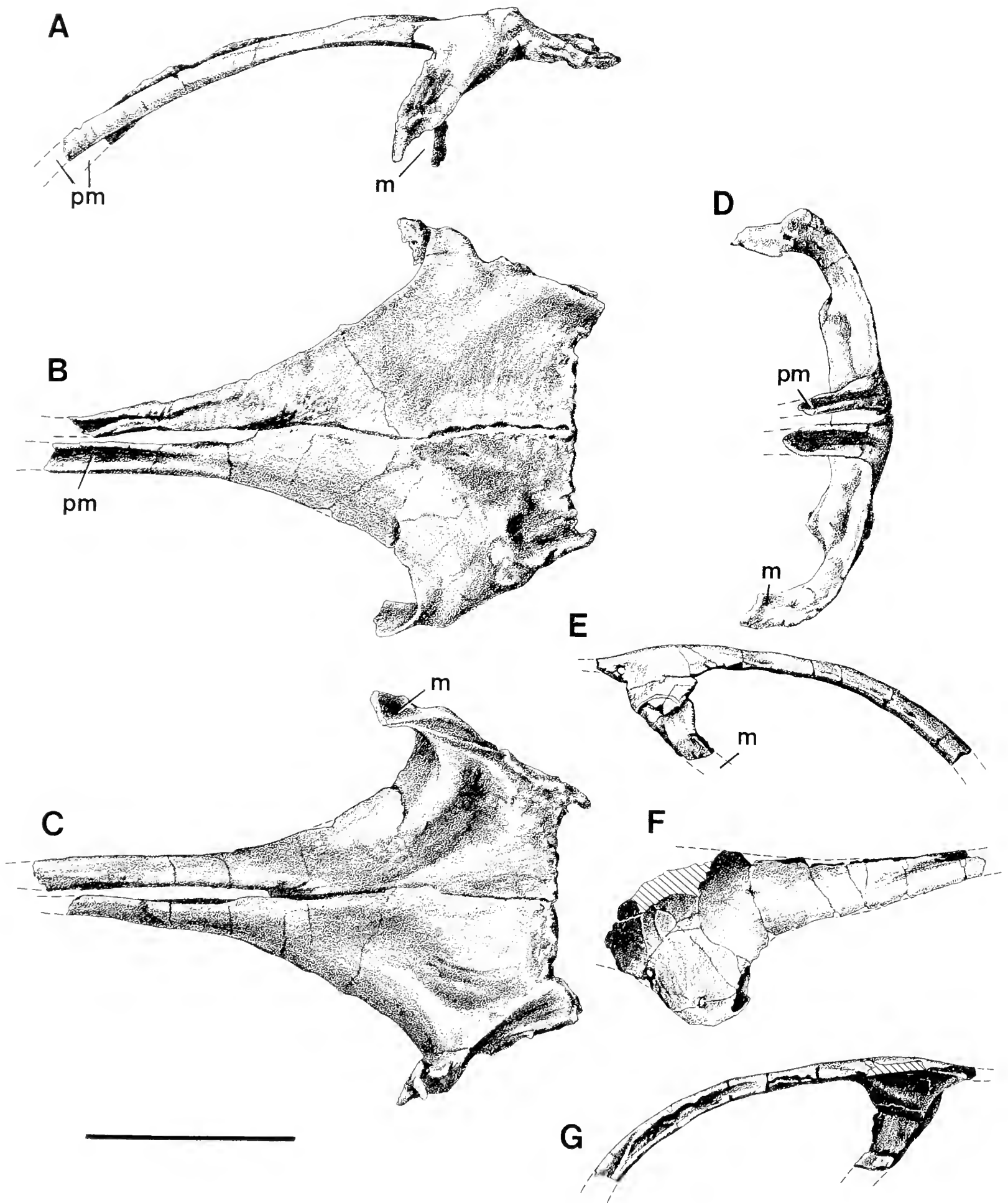


Fig. 12.—Nasals of *Camarasaurus*. A–D, *C. lentus* DNM 28 (p) (anterior to left); and E–G, *Camarasaurus* sp. UUV 3963 (r) (anterior to right). A, E, lateral; B, F, dorsal; C, ventral; D, anterior; and G, medial views. Scale = 10 cm.

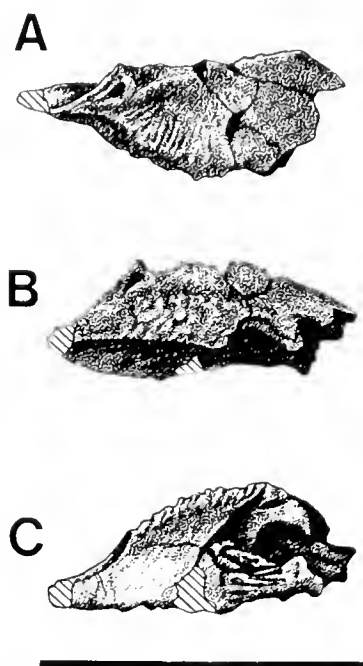


Fig. 13.—Left prefrontal of *Camarasaurus* sp. UUVP 5036. A, dorsal; B, lateral; and C, ventral views. Scale = 10 cm.

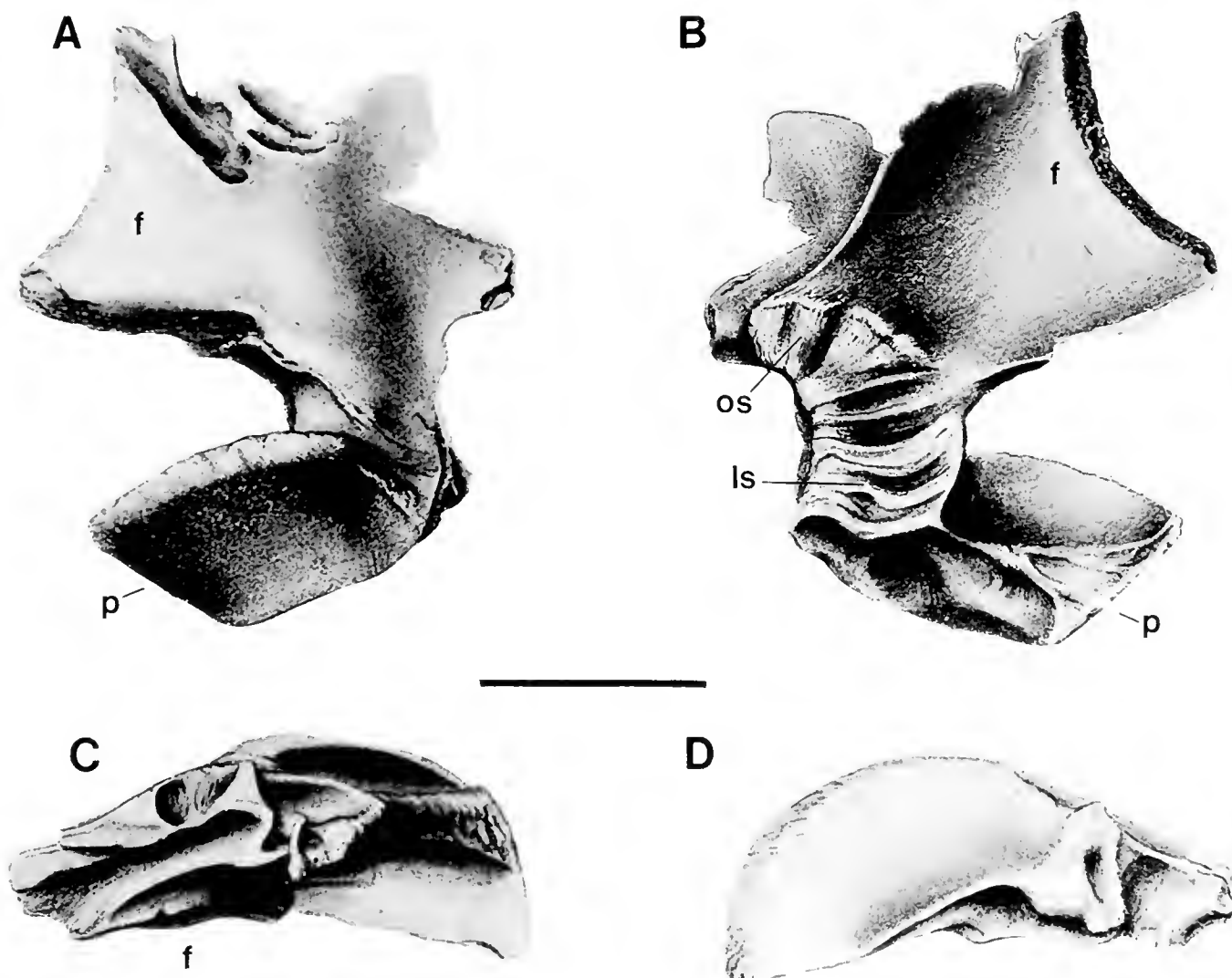


Fig. 14.—Articulated left frontal and parietal of *Camarasaurus grandis*, paratype, YPM 1905. A, dorsal; B, ventral; C, anterior; and D, posterior views. Unpublished drawings prepared under the direction of Marsh. Scale = 5 cm.

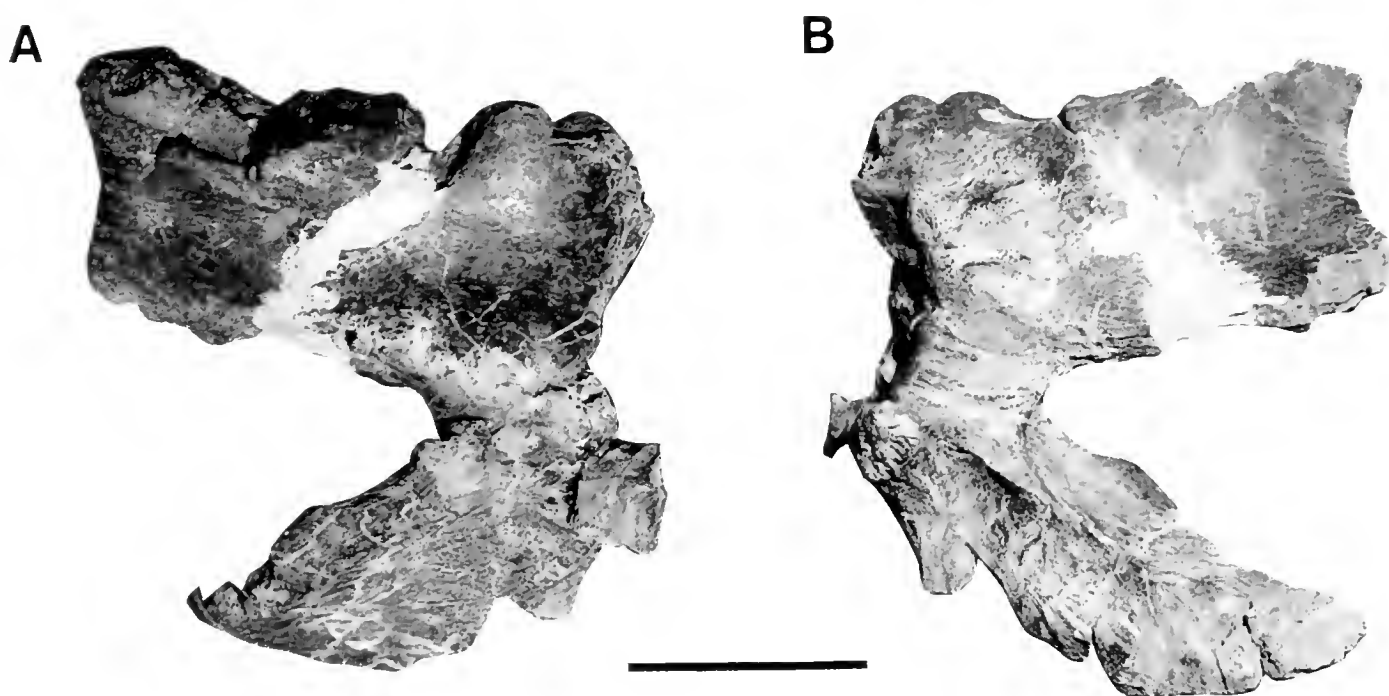


Fig. 15.—Articulated left frontal and parietal of *Camarasaurus grandis* YPM 1907. A, dorsal; and B, ventral views. Scale = 5 cm.

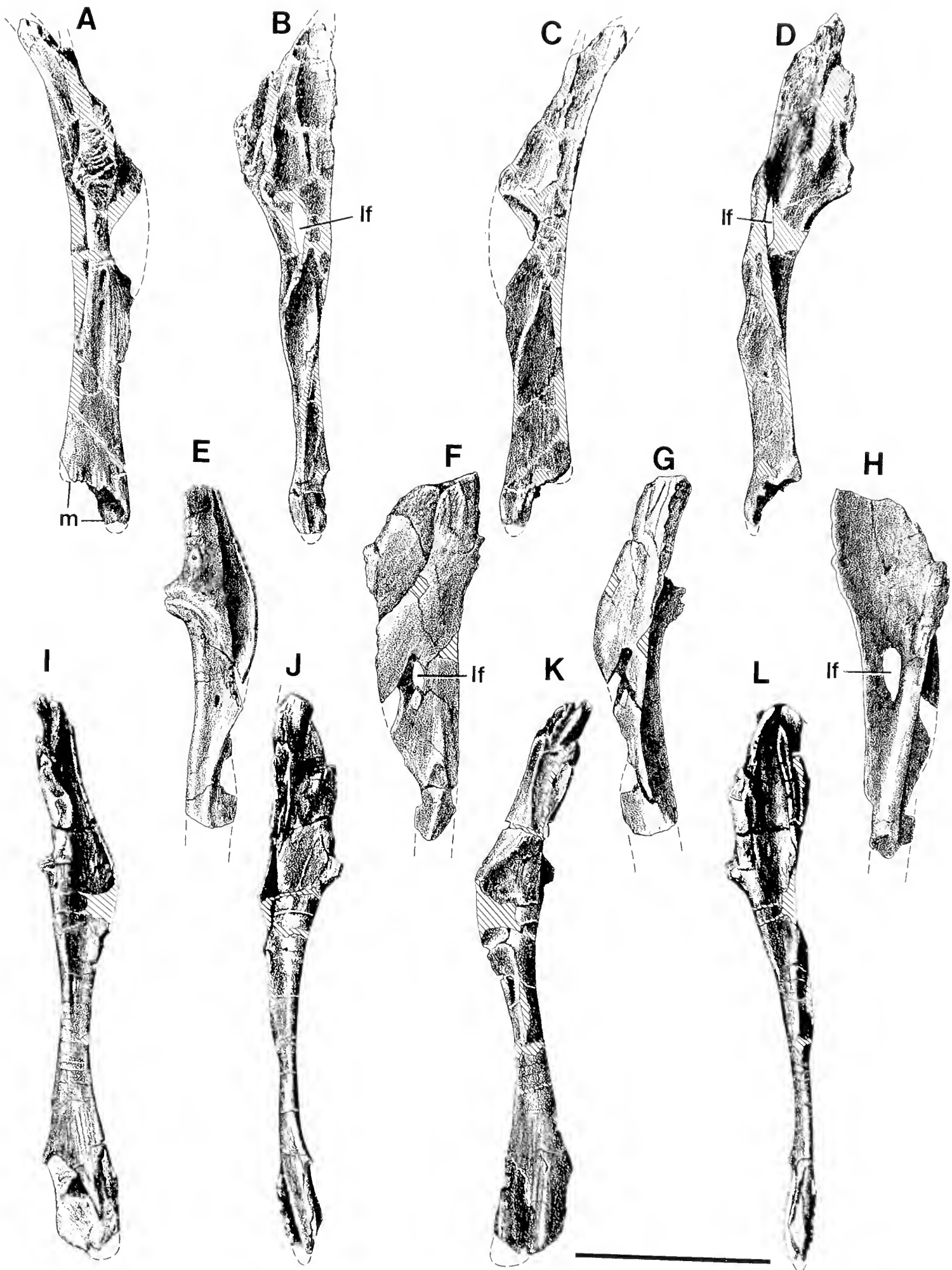


Fig. 16.—Right lacrimals of A–D, *Camarasaurus*-like skull *b* UUVP 3371; E–H, *Camarasaurus* sp. UUVP 10070; and I–L, *Camarasaurus*-like skull *a* UUVP 10795. A, E, I, lateral; B, F, J, anterior; C, G, K, medial; and D, H, L, posterior views. Scale = 10 cm.

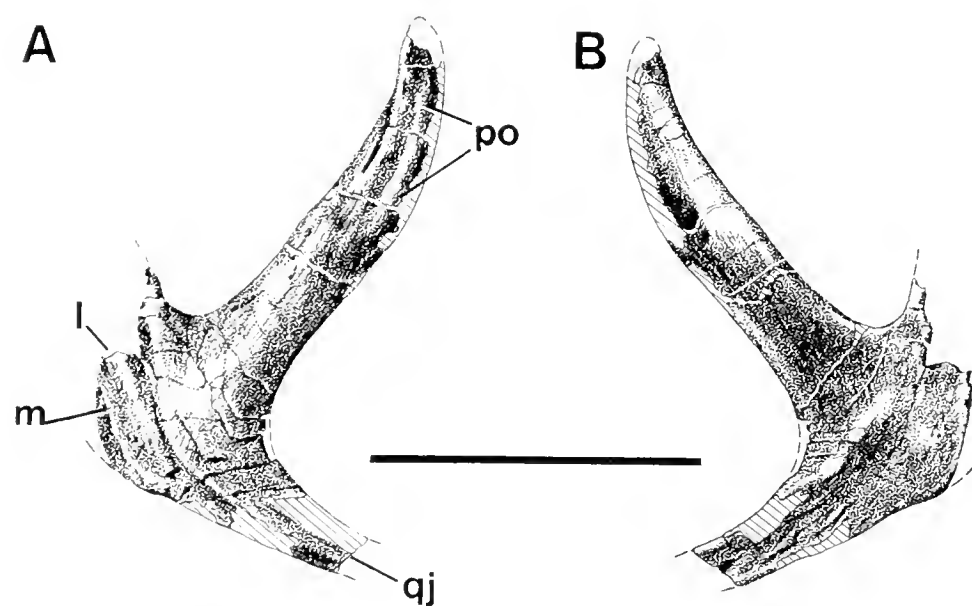


Fig. 17.—Left jugal of *Camarasaurus*-like skull a UVP 10795. A, lateral; and B, medial views. Scale = 10 cm.

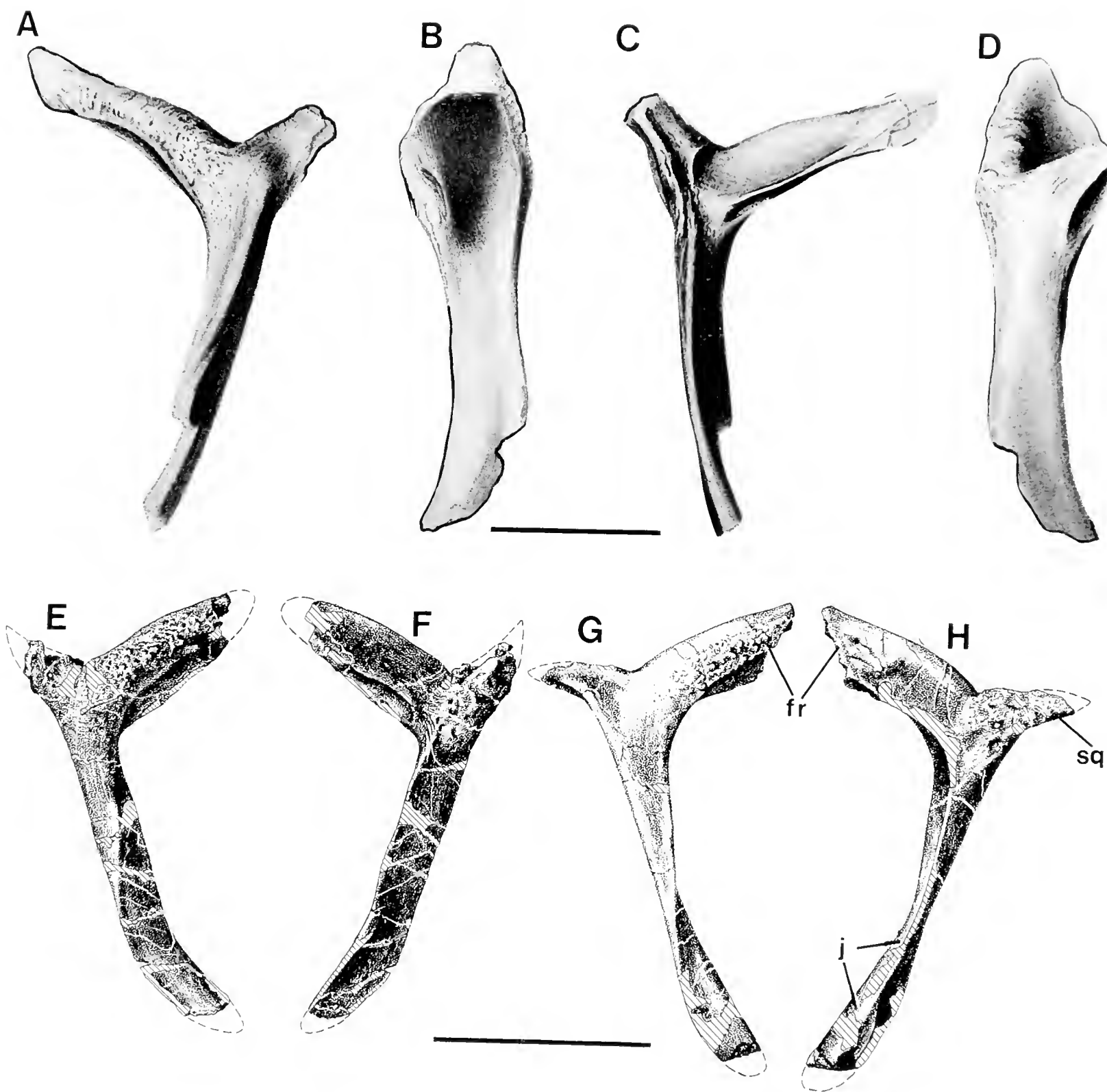


Fig. 18.—Postorbitals of A–D, *Camarasaurus grandis*, paratype, YPM 1905 (l); E, F, *Camarasaurus* sp. UUVP 5434 (r); and G, H, *Camarasaurus*-like skull a UUVP 10795 (r). A, E, G, lateral; B, anterior; C, F, H, medial; and D, posterior views. A–D, unpublished drawings prepared under the direction of Marsh. Scales, A–D = 5 cm; E–H = 10 cm.

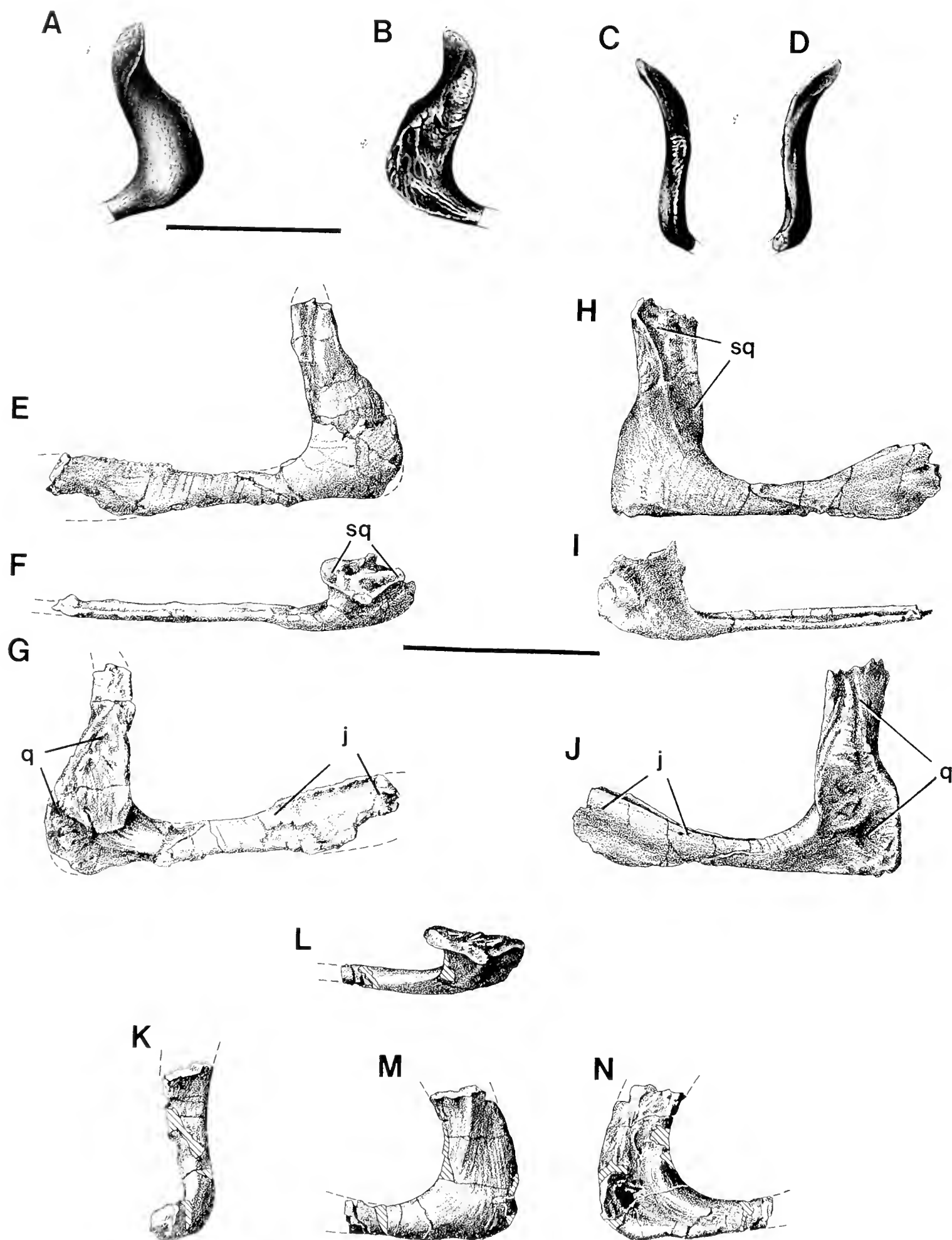


Fig. 19.—Quadratojugals of *Camarasaurus*. A–D, *C. grandis*, paratype, YPM 1905 (l); E–G, *C. lentus* DNM 28 (l); H–J, *C. lentus* DNM 975 (r); and K–N, *Camarasaurus* sp. UUVP 3293 (l). A, E, H, M, lateral; B, K, anterior; C, G, J, N, medial; D, posterior; and J, dorsal views. A–D, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviation q indicating articular surface for quadrate. Scales = 10 cm.

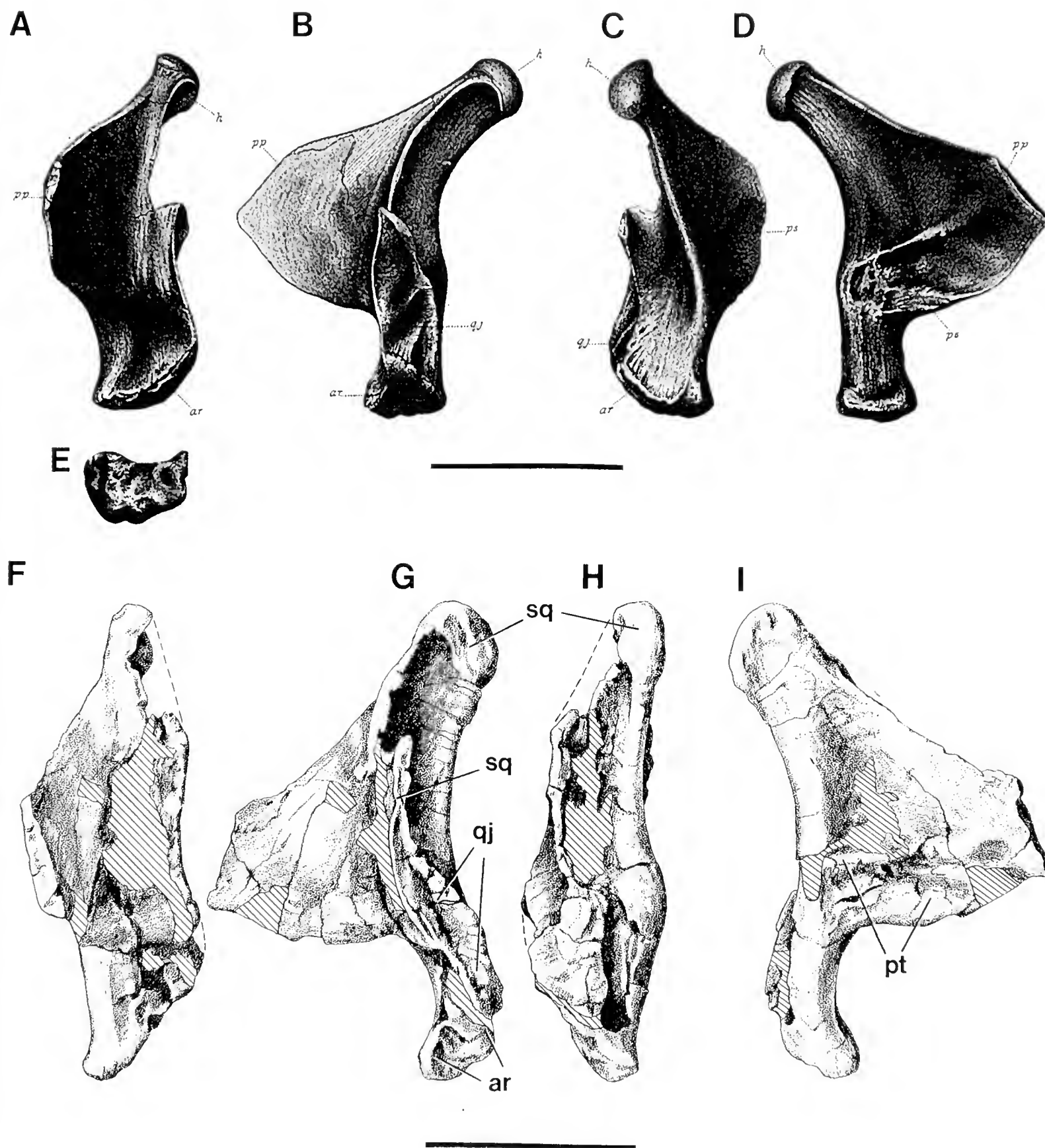


Fig. 20.—Quadrates of A–E, *Camarasaurus grandis*, paratype, YPM 1905 (l); F–I, *Camarasaurus lentus* DNM 28 (l); J–M, *Camarasaurus* sp. UUV 2625 (l); N–P, *Camarasaurus* sp. UUV 1984 (l); R–U, *Camarasaurus*-like skull *b* UUV 3638a (l); and V–Y, *Camarasaurus*-like skull *a* UUV 10795 (r). A, F, J, N, R, V, anterior; B, G, K, O, S, W, lateral; C, H, L, P, T, X, posterior; D, I, M, Q, U, Y, medial; and F, ventral views. A–D, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: h, head of quadrate; pp, pterygoid process of quadrate; ps, articular surface for pterygoid; qj, quadratojugal suture. Scales = 10 cm.

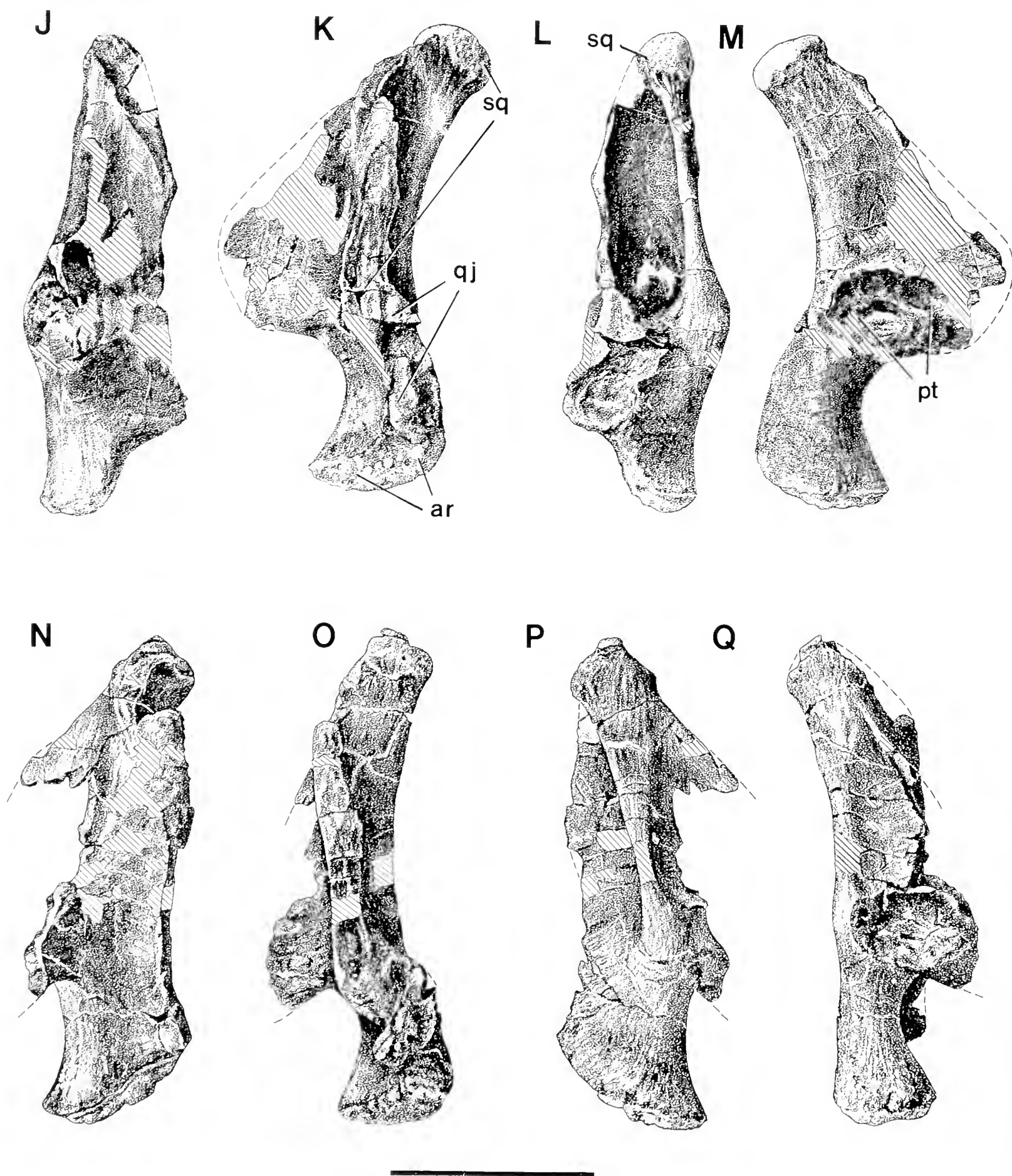


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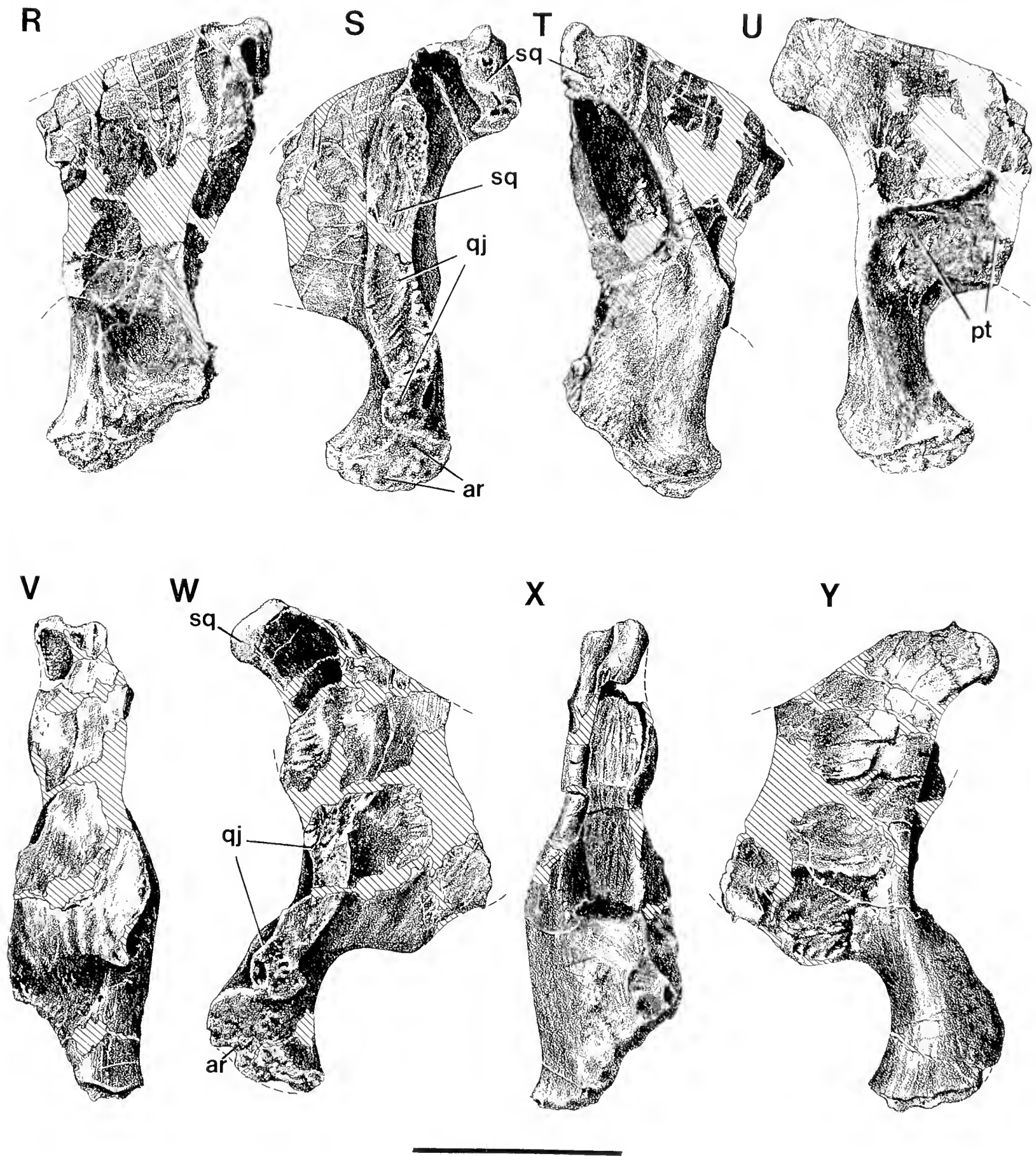


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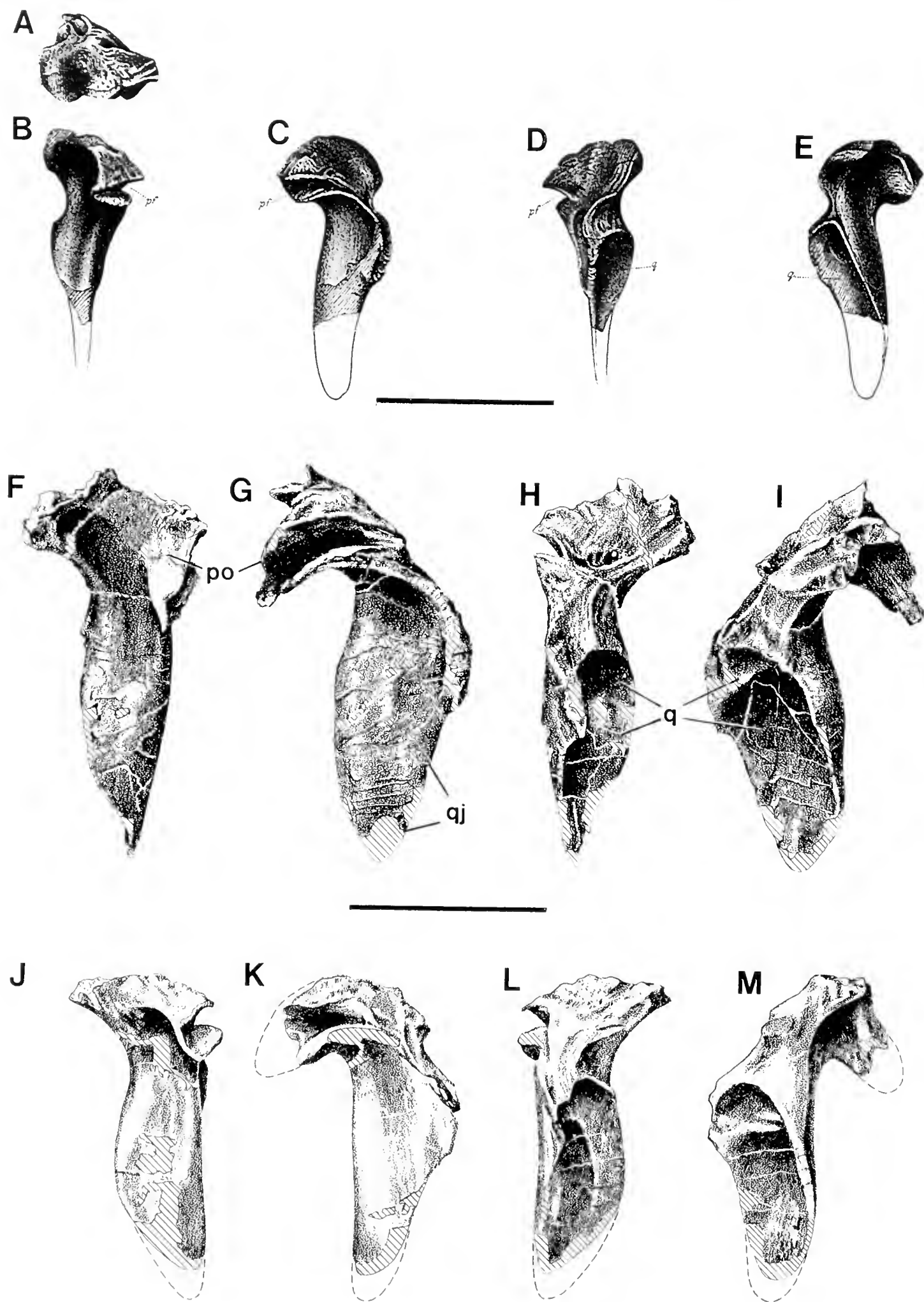


Fig. 21.—Left squamosals of A–E, *Camarasaurus grandis*, paratype, YPM 1905; F–I, *Camarasaurus* sp. UUV 5806; J–M, *Camarasaurus* sp. UUV 3507; N–Q, *Camarasaurus* sp. UUV 10064; and R–U, *Camarasaurus*-like skull a UUV 10795. A, dorsal; B, F, J, N, R, anterior; C, G, K, O, S, lateral; D, H, L, P, T, posterior; and E, I, M, Q, U, medial views. A–E, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: pf, articulation for postorbital+postfrontal; q, articular surface for quadrate. Scales = 10 cm.

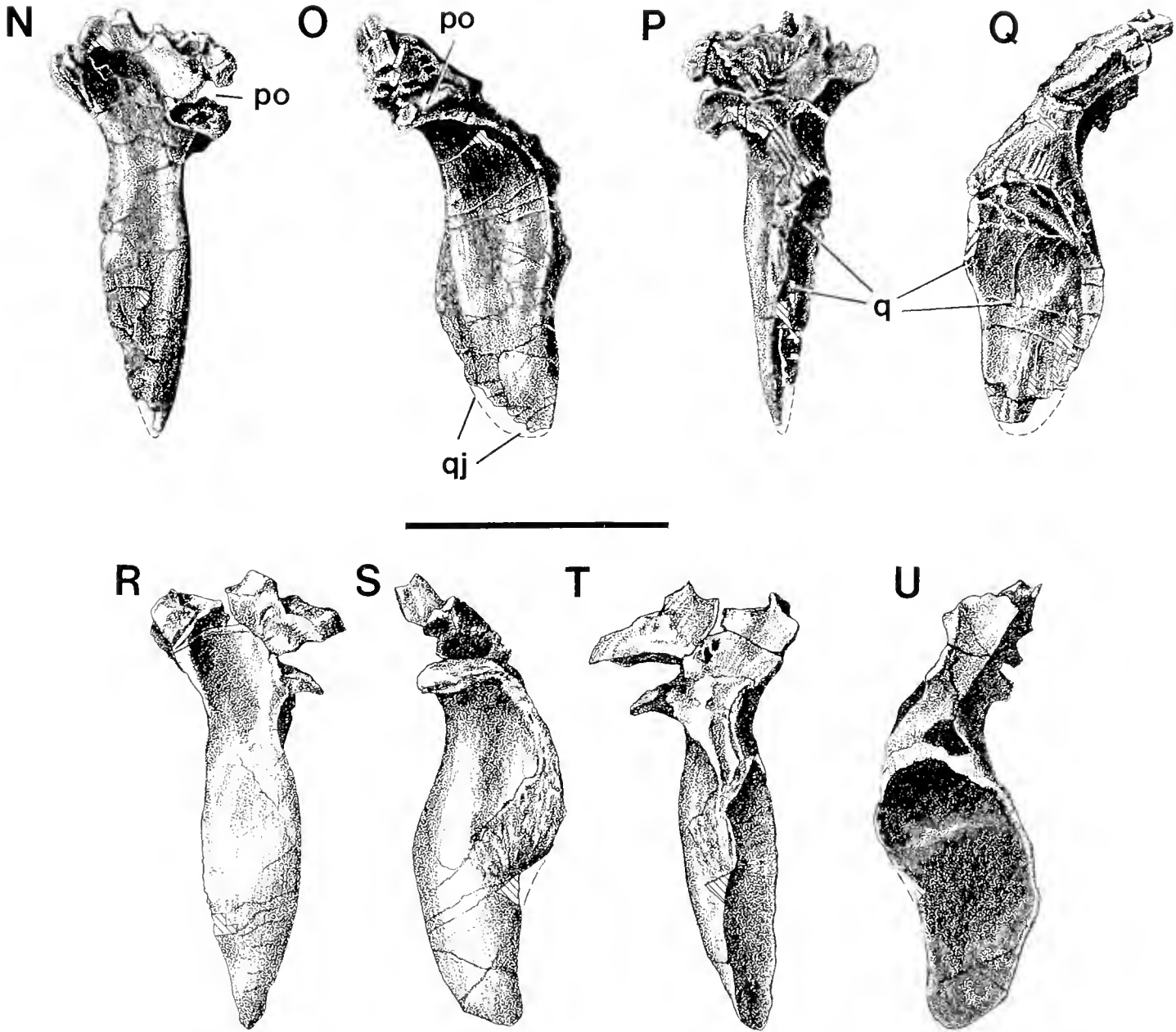


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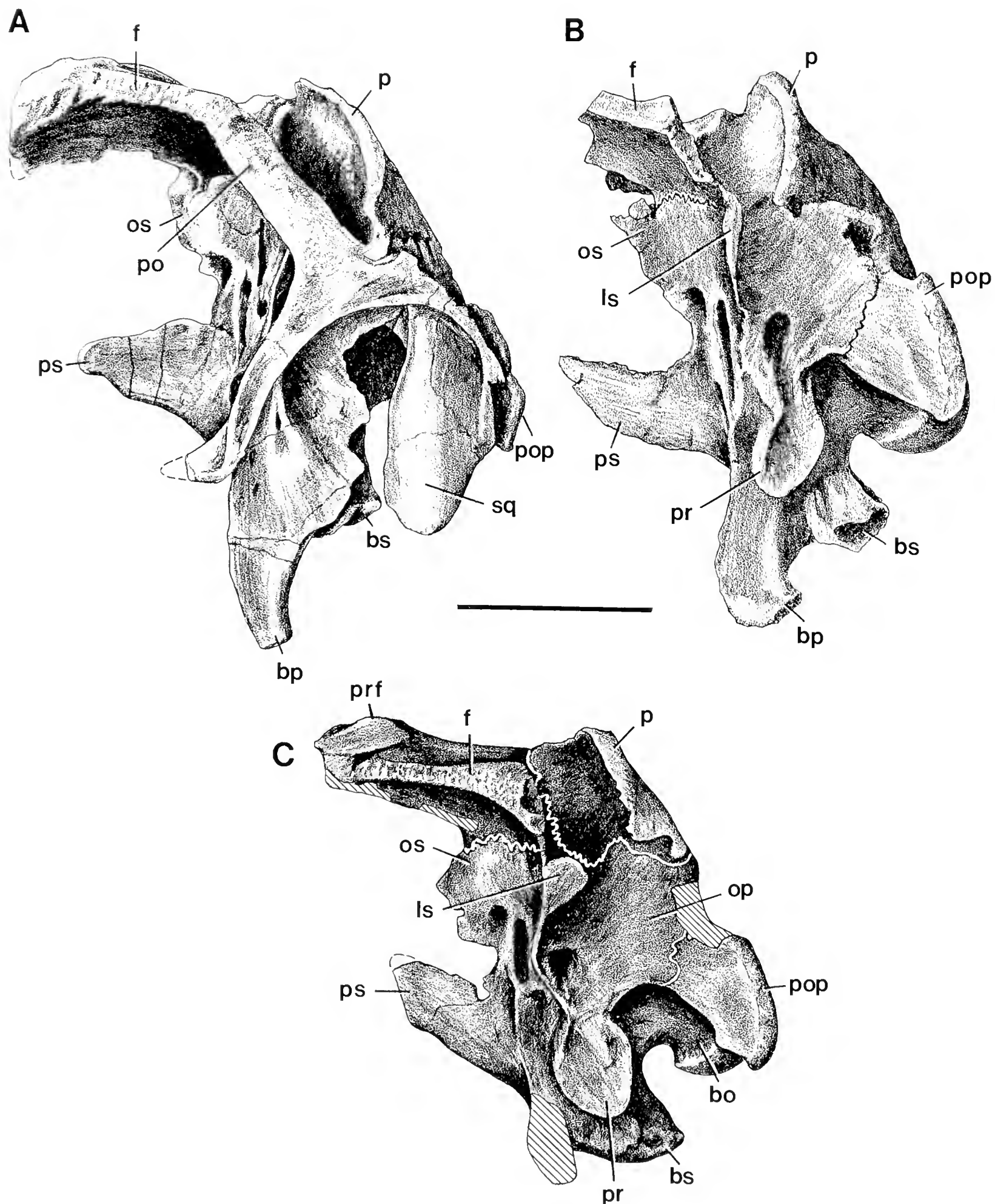


Fig. 22.—Braincases in left lateral view of A, *Camarasaurus lentus* DNM 28; B, *Camarasaurus* sp. UUV 10070; C, *Camarasaurus* sp. UUV 4286; D, *Camarasaurus* sp. UUV 3568; and E, *Camarasaurus*-like skull a UUV 10795. Scales = 10 cm.

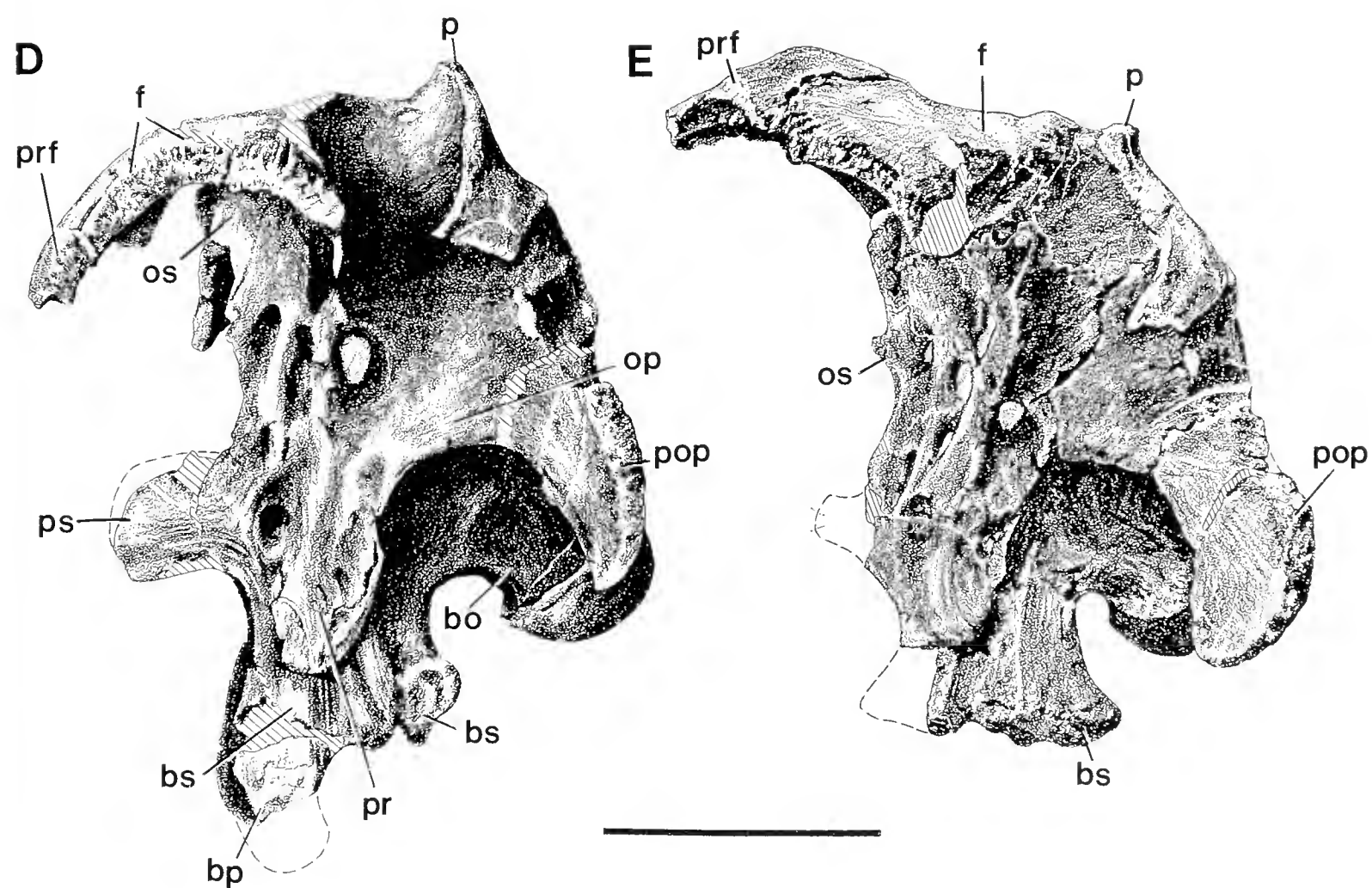


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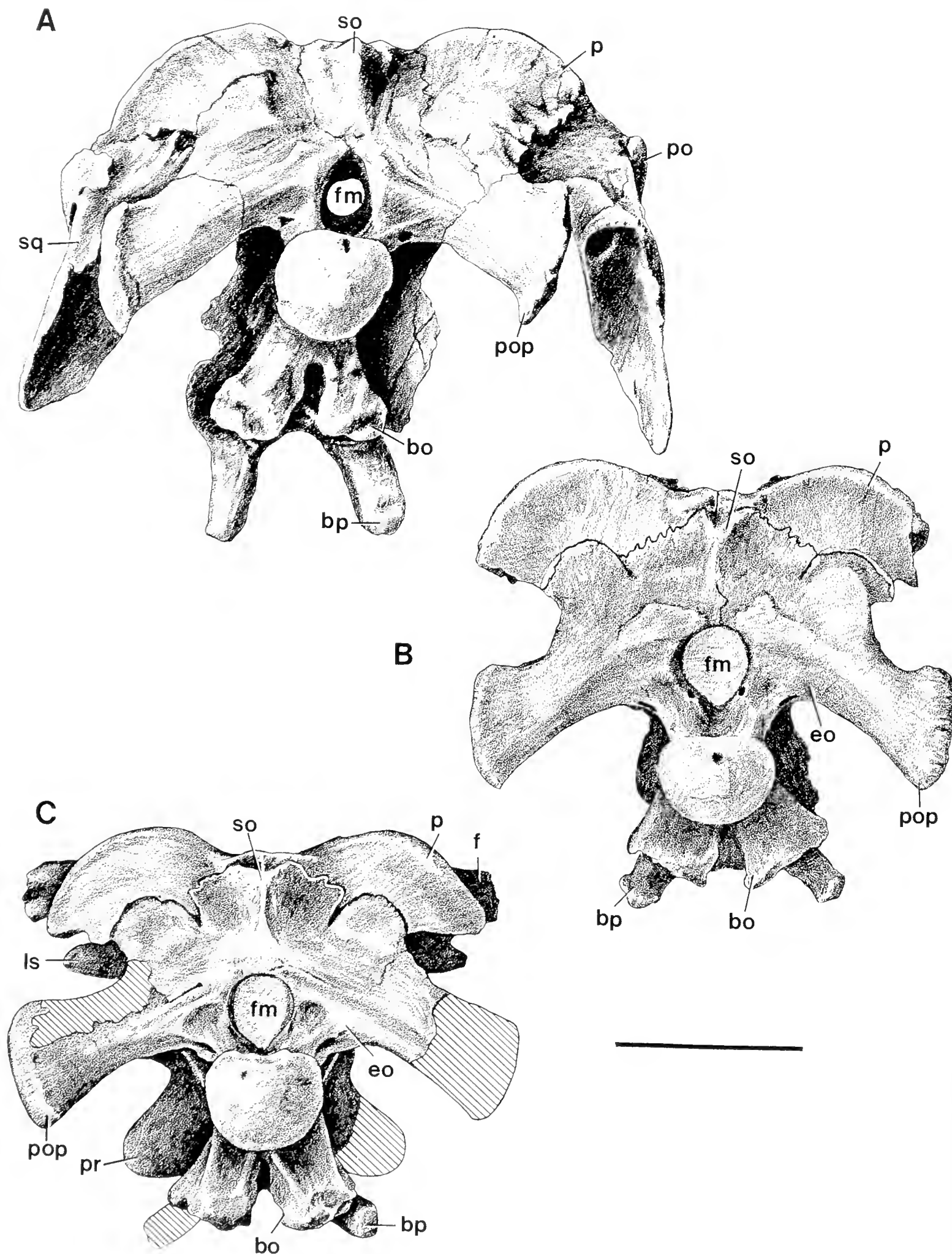


Fig. 23.—Braincases in posterior view of A, *Camarasaurus lentus* DNM 28; B, *Camarasaurus* sp. UUVP 10070; C, *Camarasaurus* sp. UUVP 4286; D, *Camarasaurus* sp. UUVP 3568; and E, *Camarasaurus*-like skull *a* UUVP 10795. Scales = 10 cm.

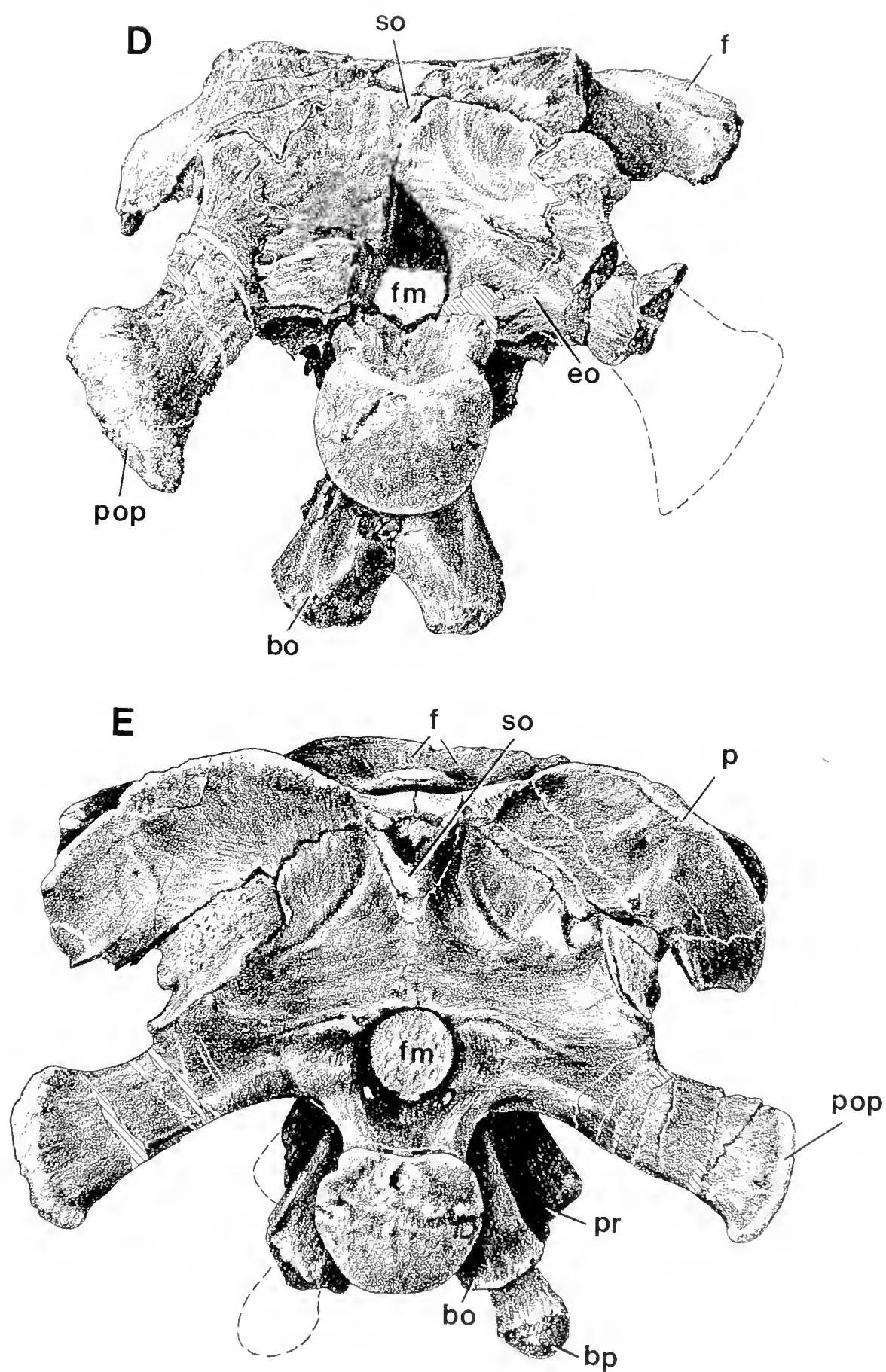


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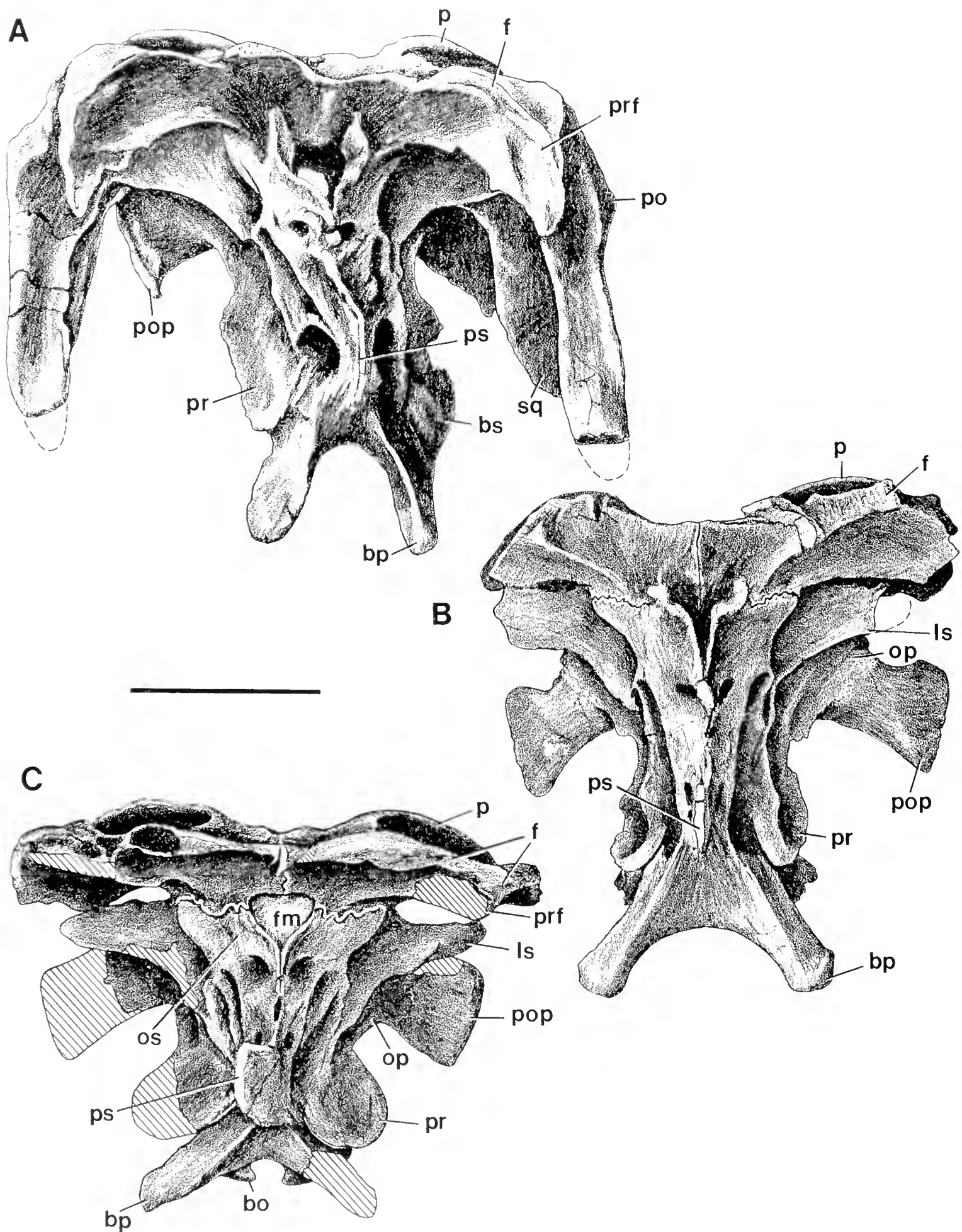


Fig. 24.—Brainscases in anterior view of A, *Camarasaurus lentus* DNM 28; B, *Camarasaurus* sp. UUV 10070; C, *Camarasaurus* sp. UUV 4286; D, *Camarasaurus* sp. UUV 3568; and E, *Camarasaurus*-like skull a UUV 10795. Scales = 10 cm.

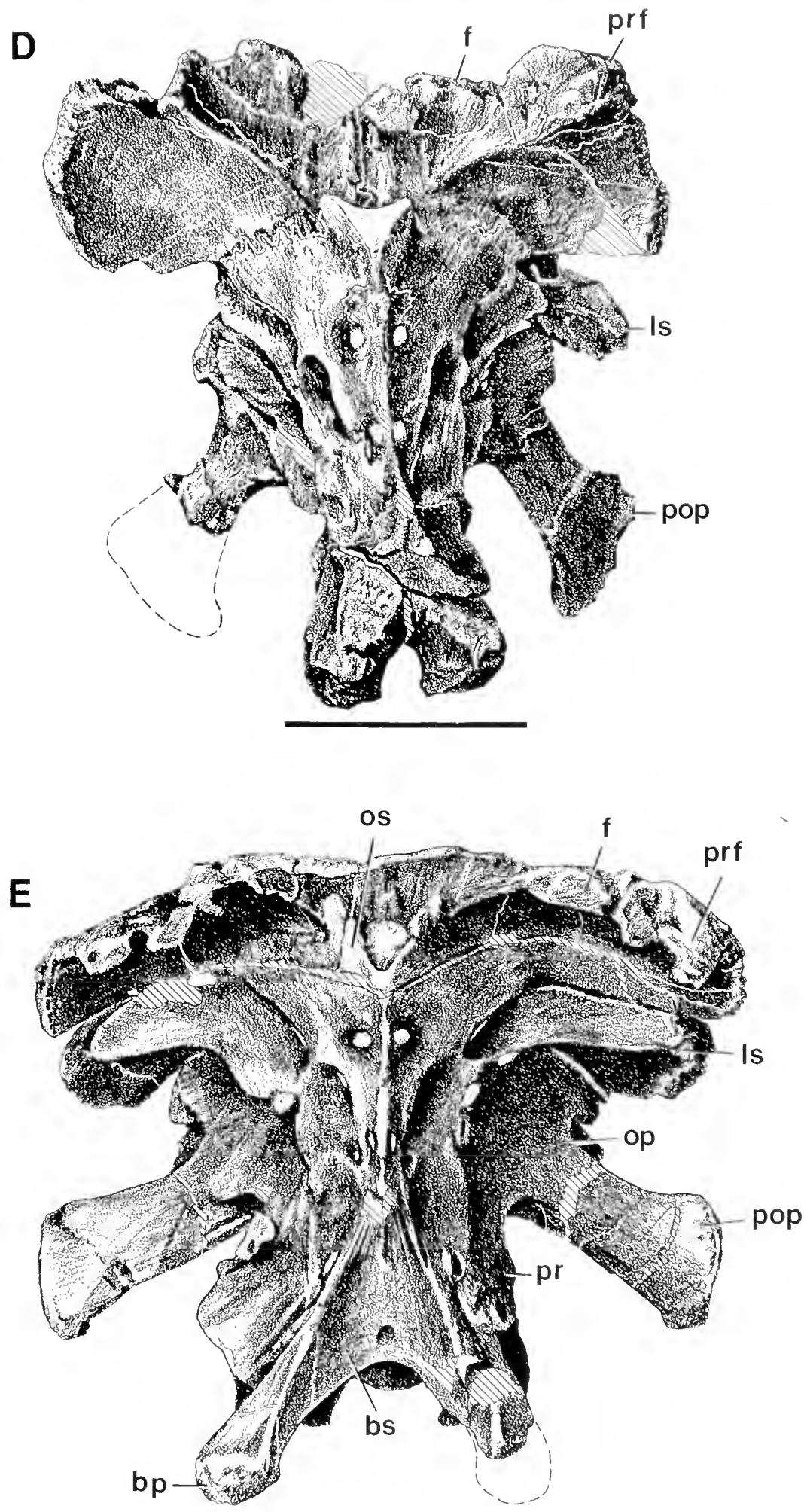


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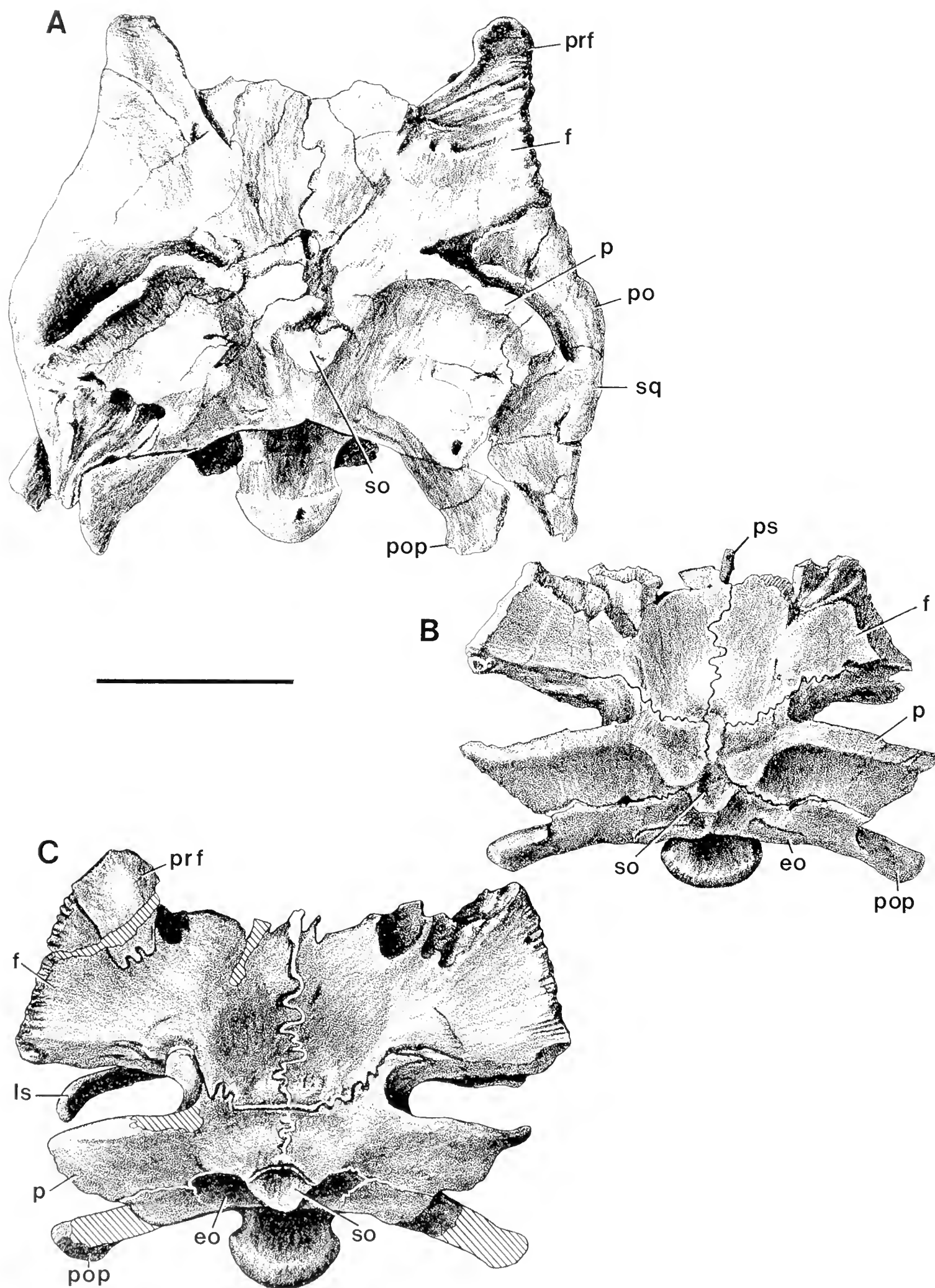


Fig. 25.—Brainscases in dorsal view of A, *Camarasaurus lentus* DNM 28; B, *Camarasaurus* sp. UUV 10070; C, *Camarasaurus* sp. UUV 4286; D, *Camarasaurus* sp. UUV 3568; and E, *Camarasaurus*-like skull a UUV 10795. Scales = 10 cm.

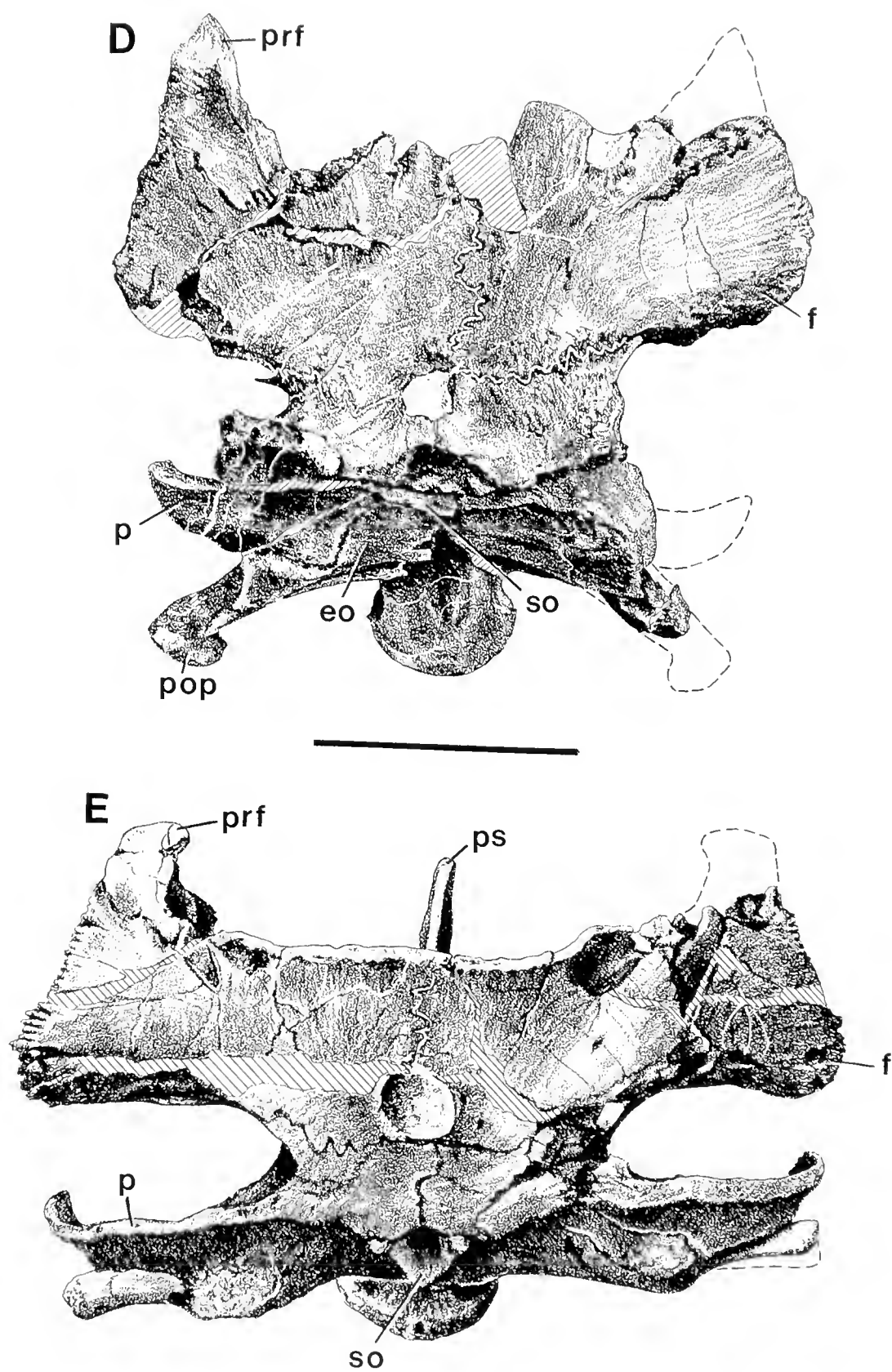


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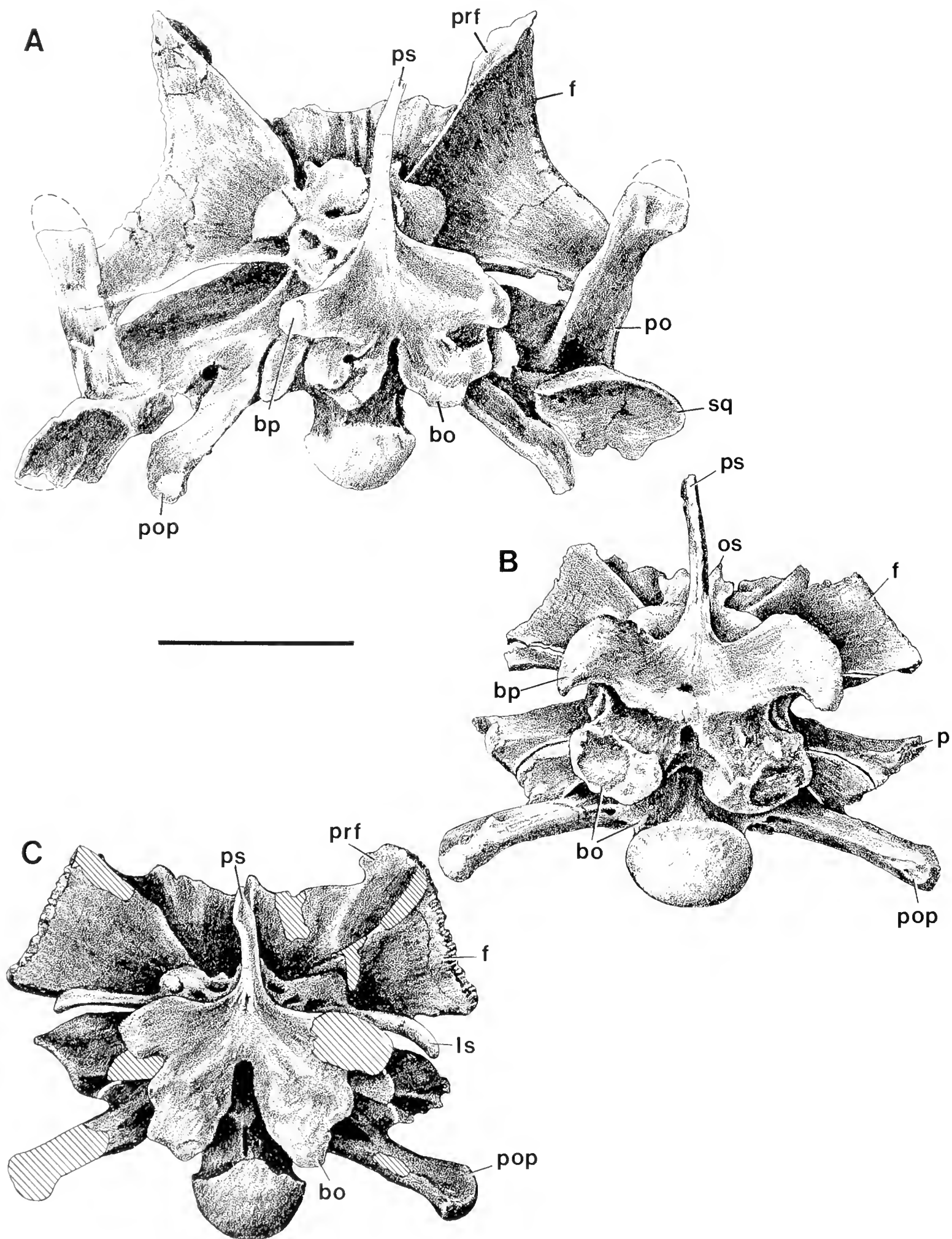


Fig. 26.—Brainscases in ventral view of A, *Camarasaurus lentus* DNM 28; B, *Camarasaurus* sp. UUV 10070; D, *Camarasaurus* sp. UUV 4286; D, *Camarasaurus* sp. UUV 3568; and E, *Camarasaurus*-like skull a UUV 10795. Scales = 10 cm.

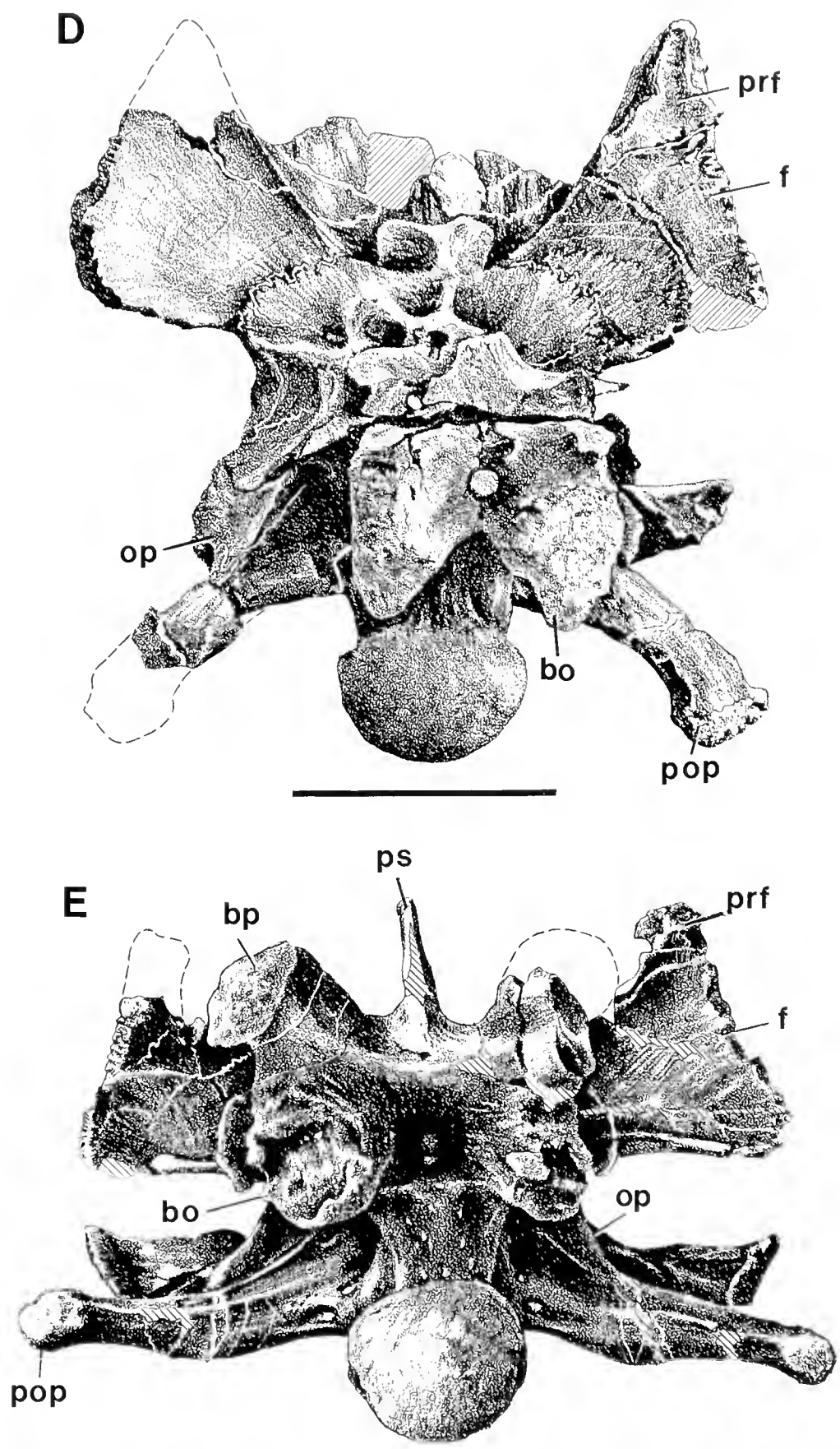


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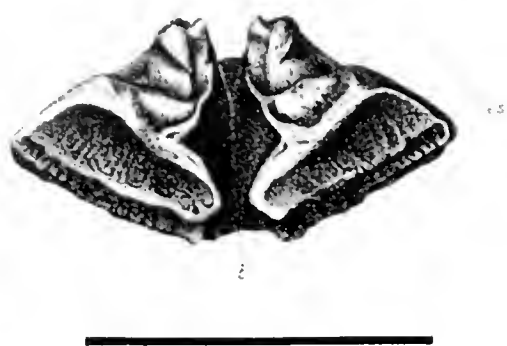


Fig. 27.—Supraoccipital of *Camarasaurus grandis*, paratype, YPM 1905 in anteroventral view. Drawing prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: b, endocranial cavity; es, exoccipital suture. Scale = 10 cm.

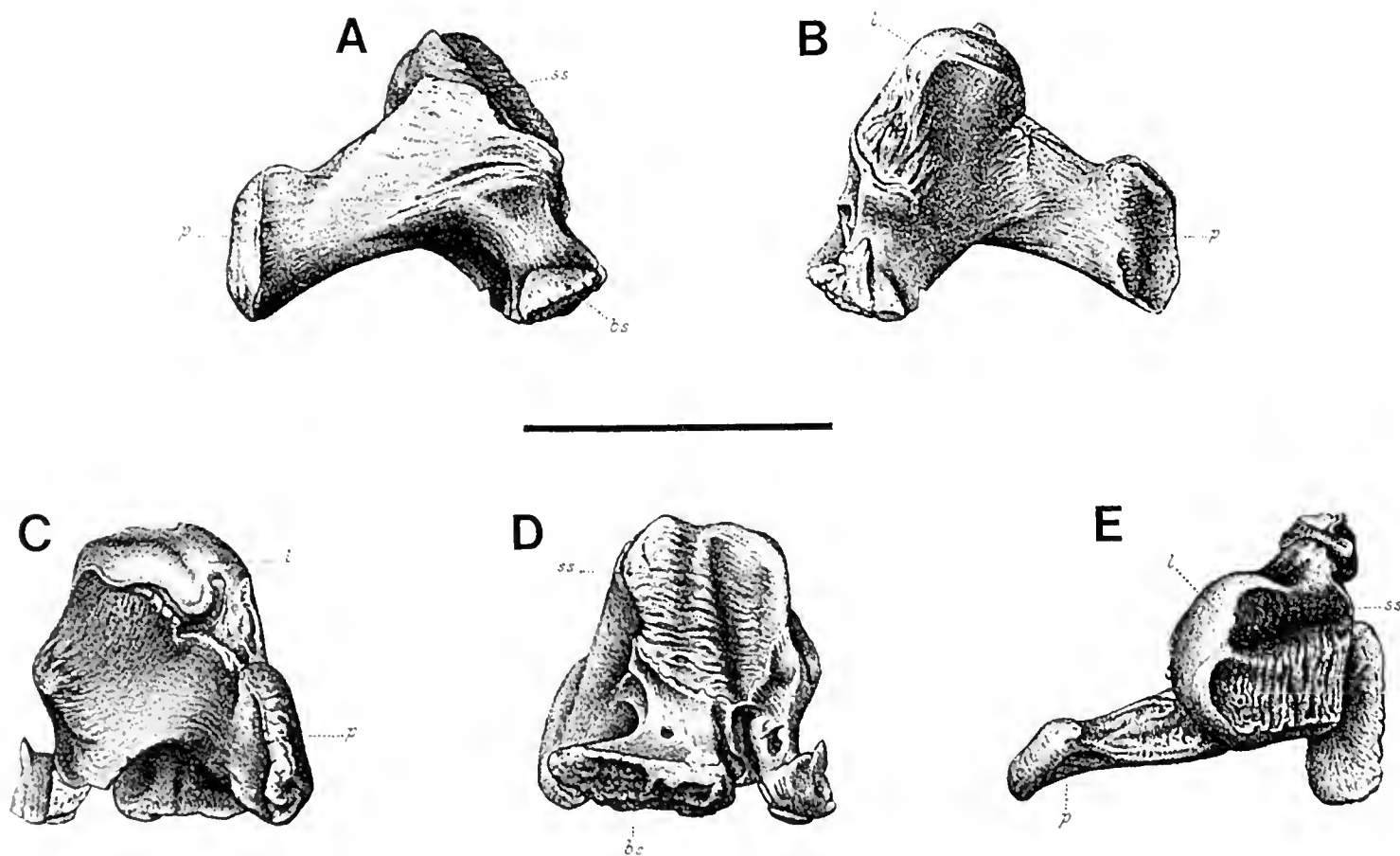


Fig. 28.—Articulated left prootic and exoccipital-opisthotic complex of *Camarasaurus grandis*, paratype, YPM 1905. A, posterior; B, anterior; C, lateral; D, medial; and E, dorsal views. Drawings prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: bs, basisphenoid suture; l, lateral wall of braincase; p, paroccipital process; ss, supraoccipital suture. Scale = 10 cm.



Fig. 29.—Right exoccipital-opisthotic complex of *Camarasaurus grandis* YPM 1912. A, anterior; B, medial; and C, posterior views. Scale = 5 cm.

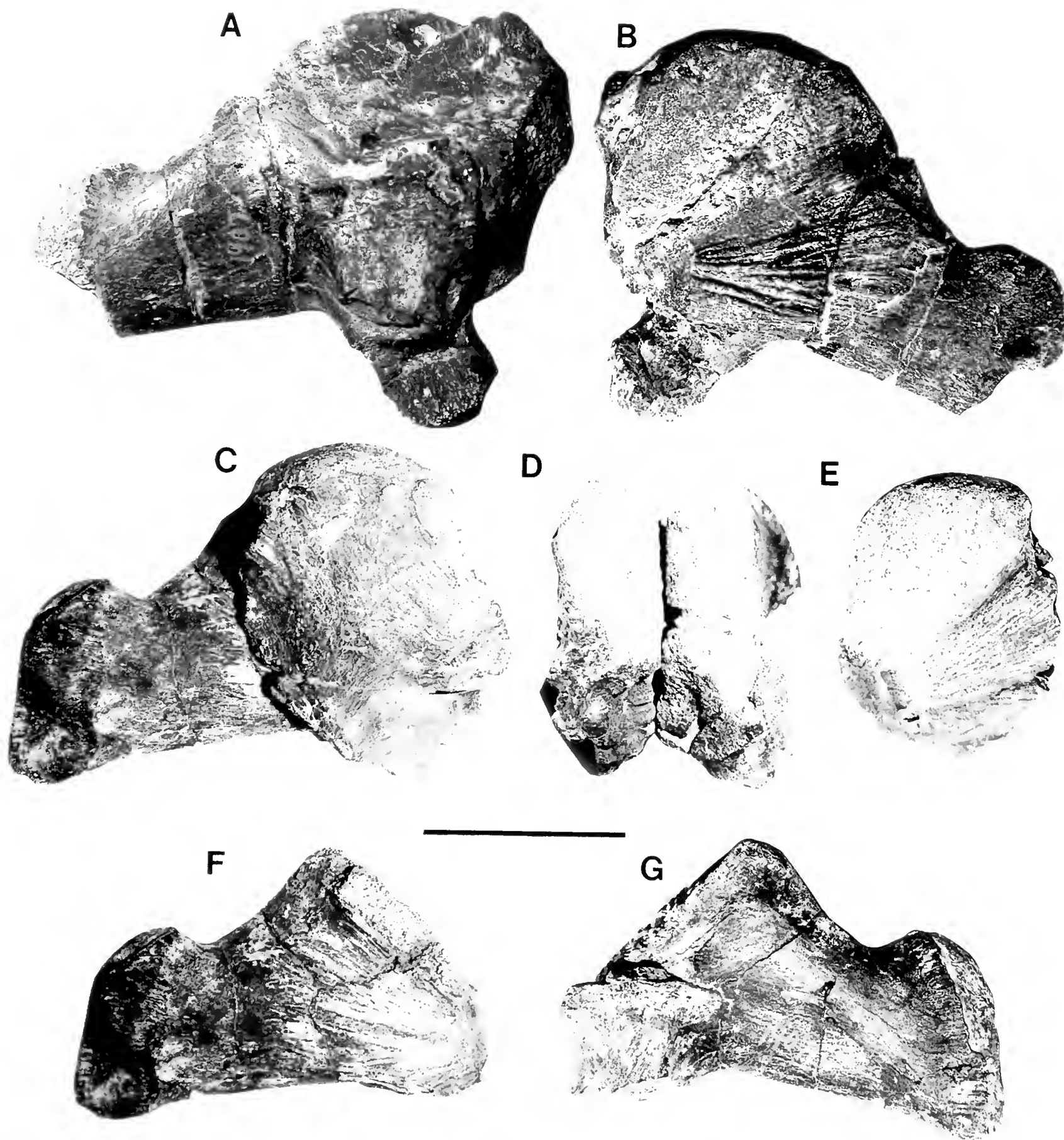


Fig. 30.—Braincase bones of *Camarasaurus grandis* YPM 1907. A, posterior; and B, anterior views of left exoccipital–opisthotic complex with fragment of supraoccipital of large skull included in YPM 1907. C, anterior; and D, medial views of right exoccipital–opisthotic complex and prootic of small skull included in YPM 1907. E, posterior view of right prootic of C, D. F, anterior; and G, posterior views of exoccipital–opisthotic complex of C, D. Scale = 5 cm.

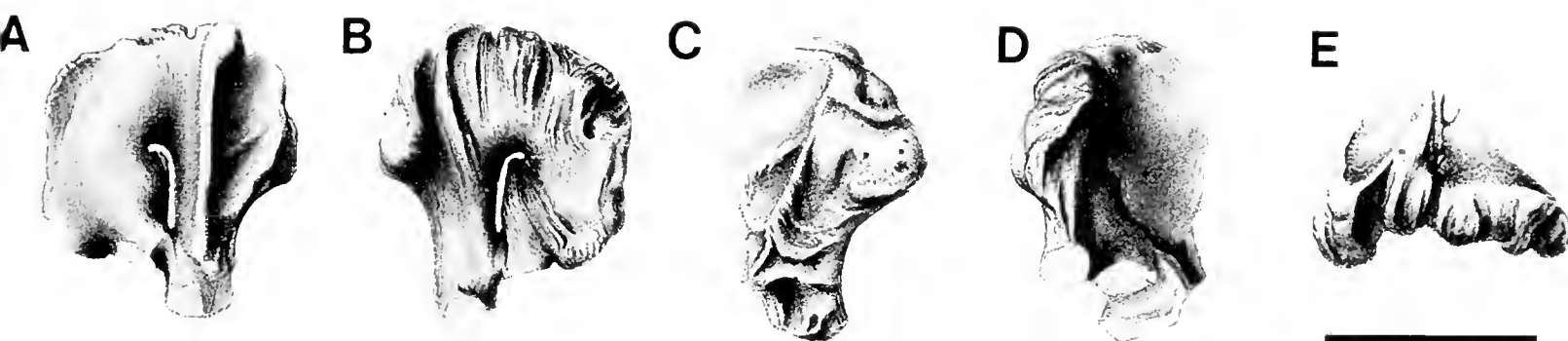


Fig. 31.—Left orbitosphenoid–laterosphenoid complex of *Camarasaurus grandis* YPM 1907. A, lateral; B, medial; C, posterior; D, anterior; and E, dorsal views. Unpublished drawings prepared under the direction of Marsh. Scale = 5 cm.

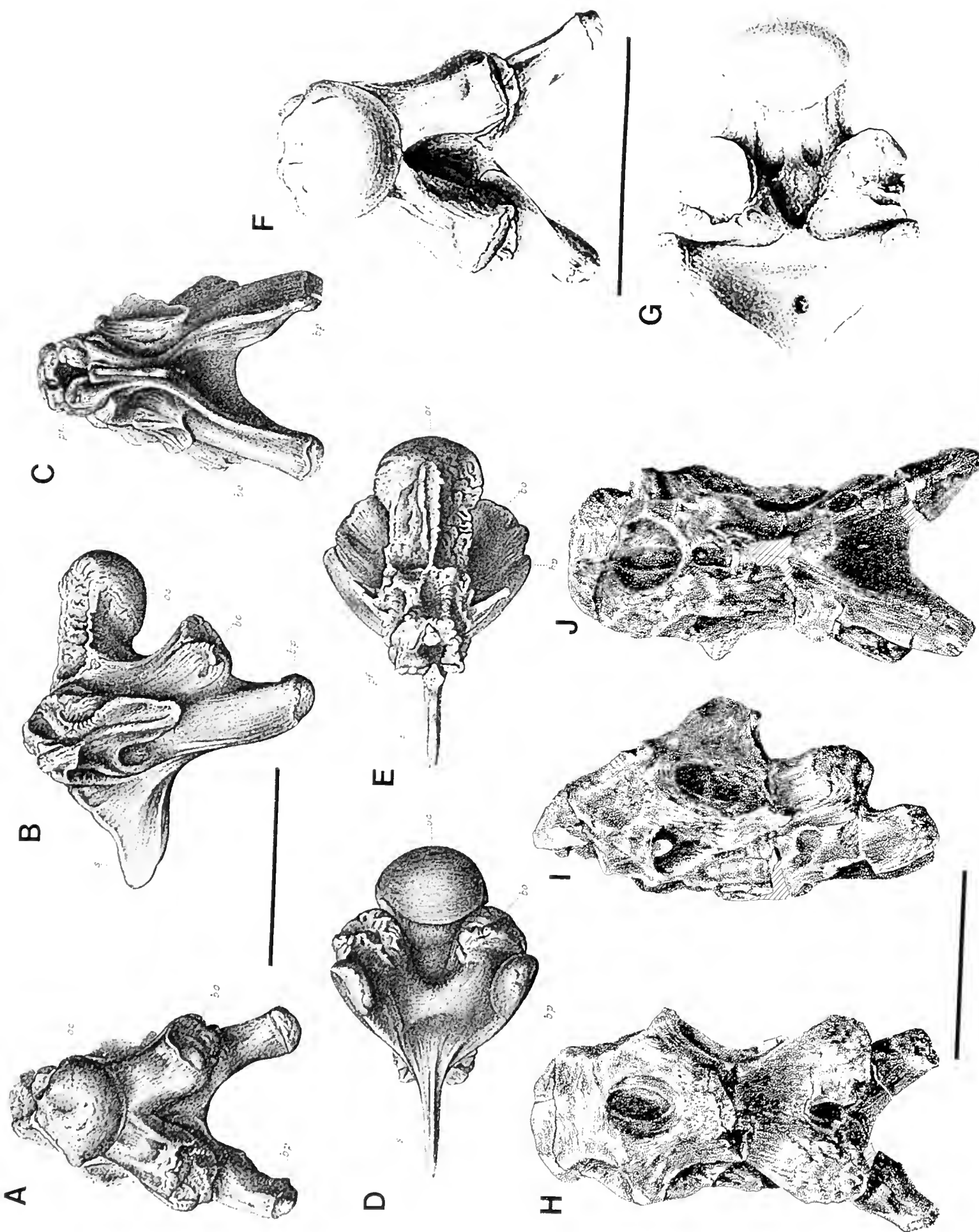


Fig. 32.—Basioccipital-basisphenoid-parasphenoid complexes of *Camarasaurus*. A–E, *Camarasaurus grandis*, paratype, YPM 1905; F, G, *C. grandis*, holotype, YPM 1901; H–J, *Camarasaurus* sp. UUVP 5684. A, F, H, posterior; B, I, left lateral; C, J, anterior; D, G, ventral; and E, dorsal views. A–E, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: bo, basioccipital tubercle; bp, basipterygoid process; oc, occipital condyle; pf, pituitary fossa; s, parasphenoid. F, G, unpublished drawings prepared under the direction of Marsh. Scales = 10 cm.

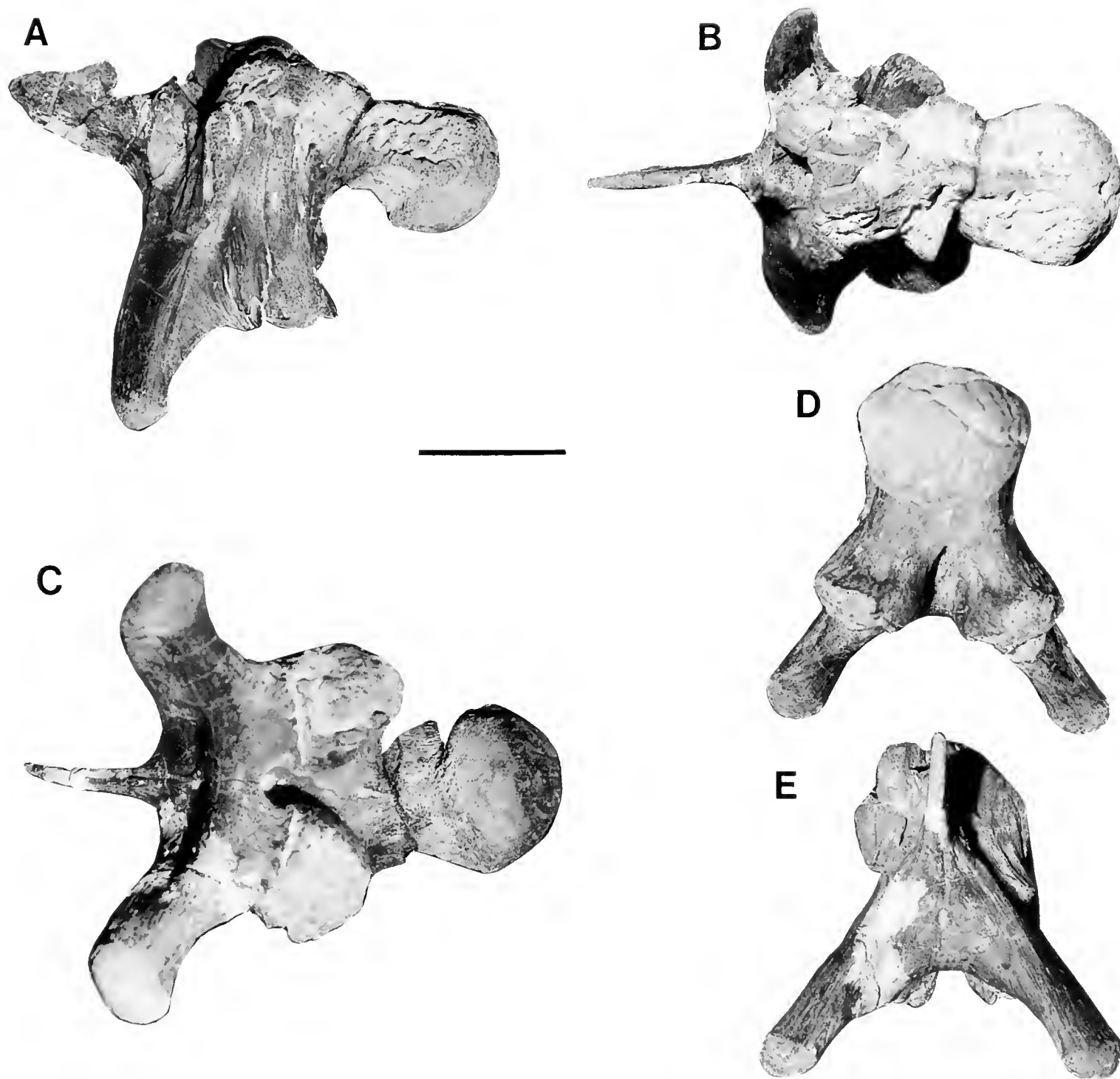


Fig. 33.—Basioccipital-basisphenoid-parasphenoid complex of *Camarasaurus grandis* YPM 1907. A, left lateral; B, dorsal; C, ventral; D, posterior; and E, anterior views. Scale = 5 cm.

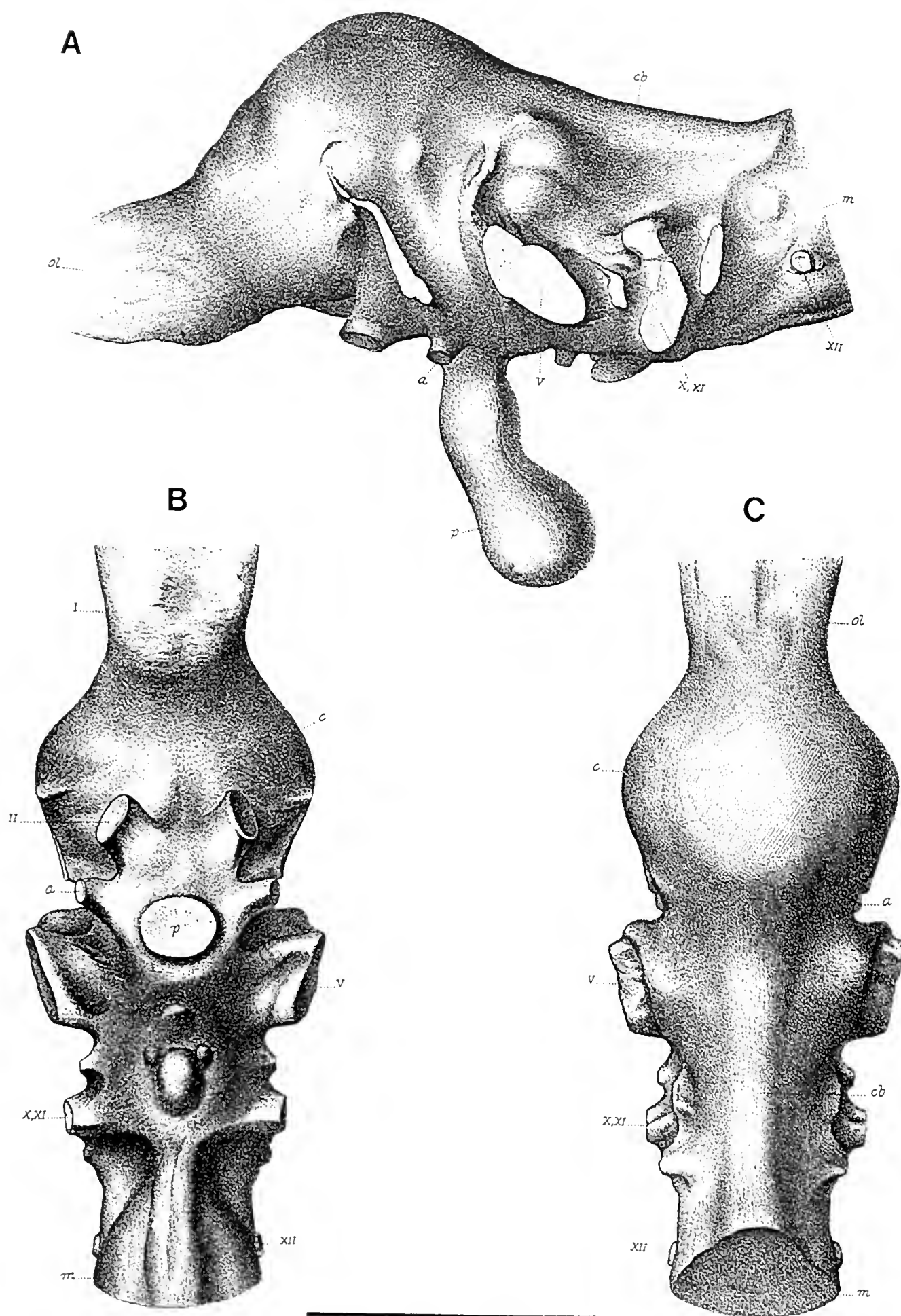


Fig. 34.—Endocranial cast of *Camarasaurus grandis*, paratype, YPM 1905. A, left lateral; B, ventral; C, dorsal views. Drawings prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: a, artery; c, cerebrum; cb, cerebellum; m, medulla; ol, olfactory stalk; p, pituitary body; I, olfactory nerve; II, optic nerve; V, trigeminal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. Scale = 5 cm.

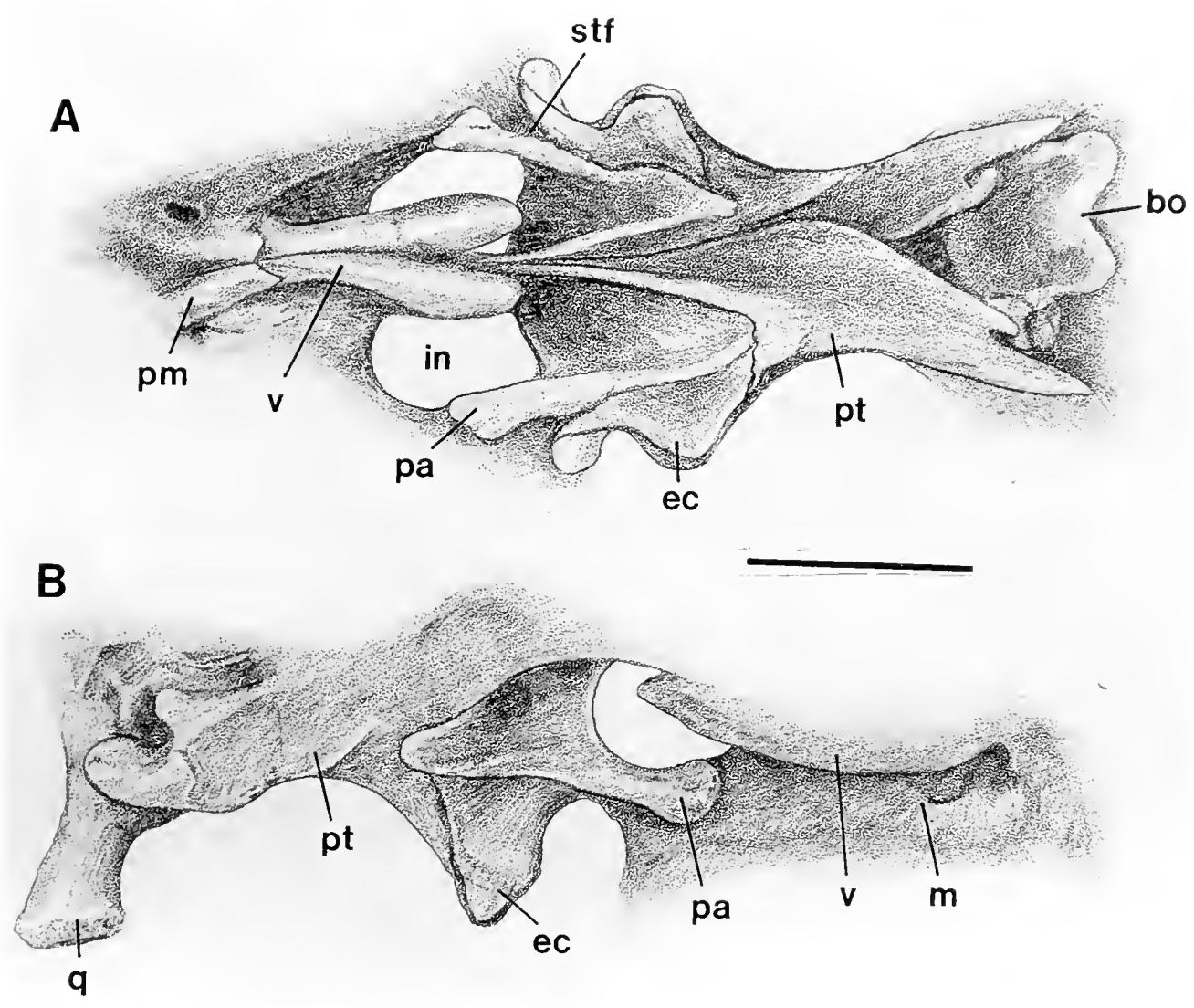


Fig. 35.—Palate of *Camarasaurus lentus* CM 11338. A, ventral; and B, medial views of left side. Scale = 5 cm.

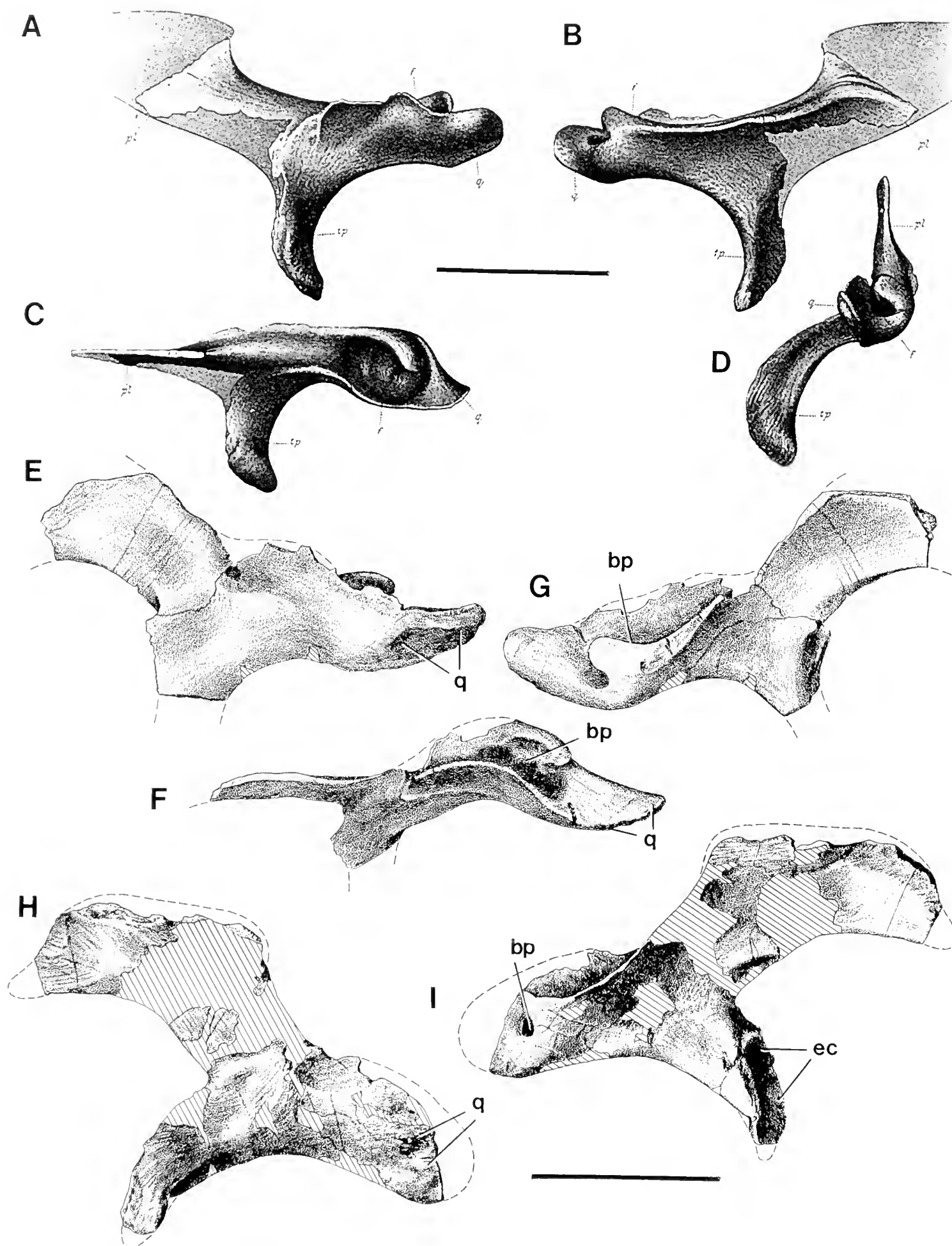


Fig. 36.—Pterygoids of A–D, *Camarasaurus grandis*, paratype, YPM 1905 (l); E–G, *Camarasaurus* sp. UUVP 10071 (l); H, I, *Camarasaurus* sp. UUVP 3350 (l); J–M, *Camarasaurus lentus* DNM 28 (l); N–P, *Camarasaurus lentus* DNM 975 (r); Q–U, *Camarasaurus*-like skull a UUVP 10795 (r); V–Y, *Camarasaurus* sp. UUVP 1986 (r). A, E, H, J, N, S, W, lateral; B, G, I, K, T, X, medial; C, F, L, P, Q, V, dorsal; R, ventral; D, posterior; and M, O, U, Y, anterior views. A–E, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: f, fossa for basipterygoid process; pl, palatine process of pterygoid; q, articular surface of quadrate; tp, pterygoid flange. Scales = 10 cm.

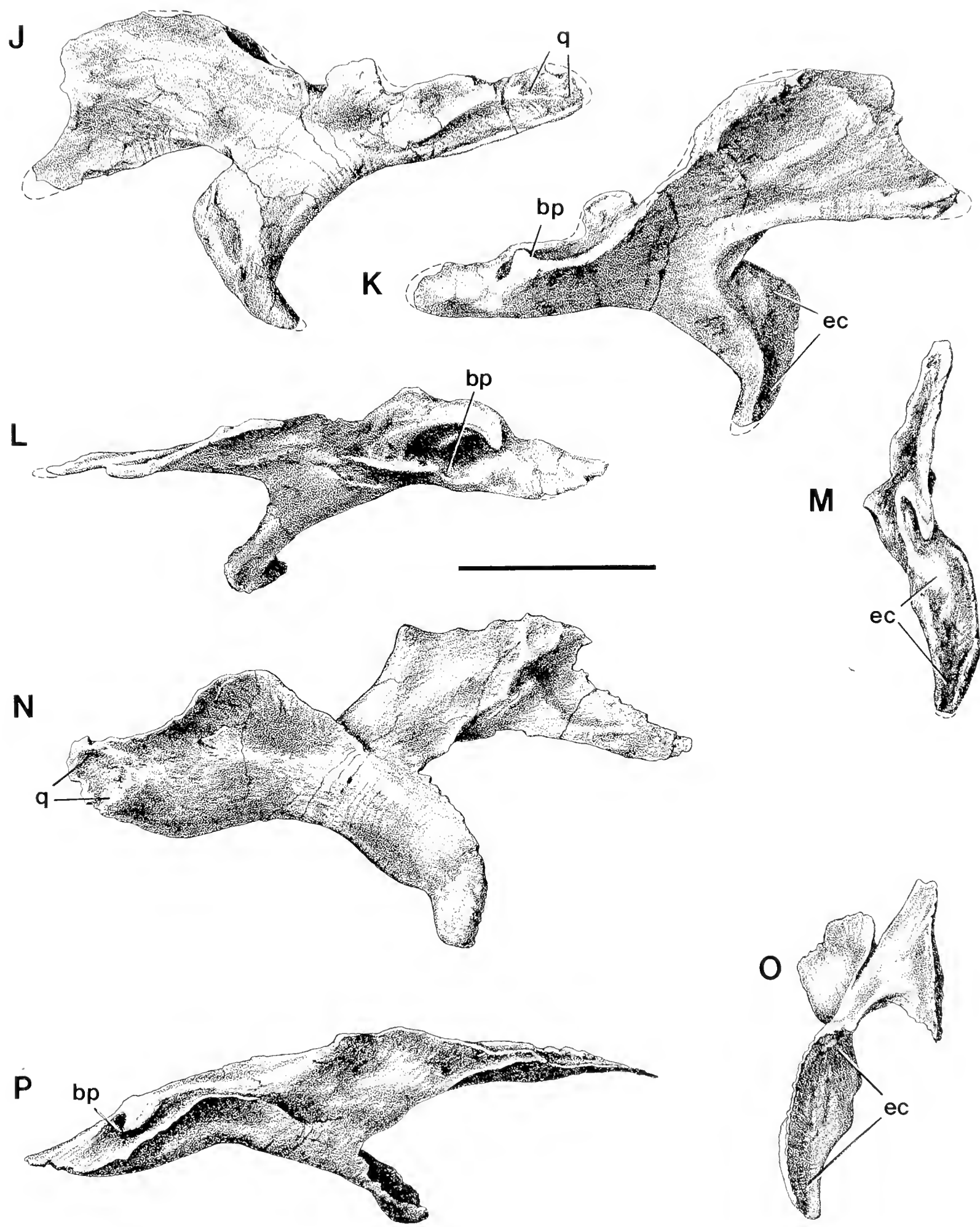


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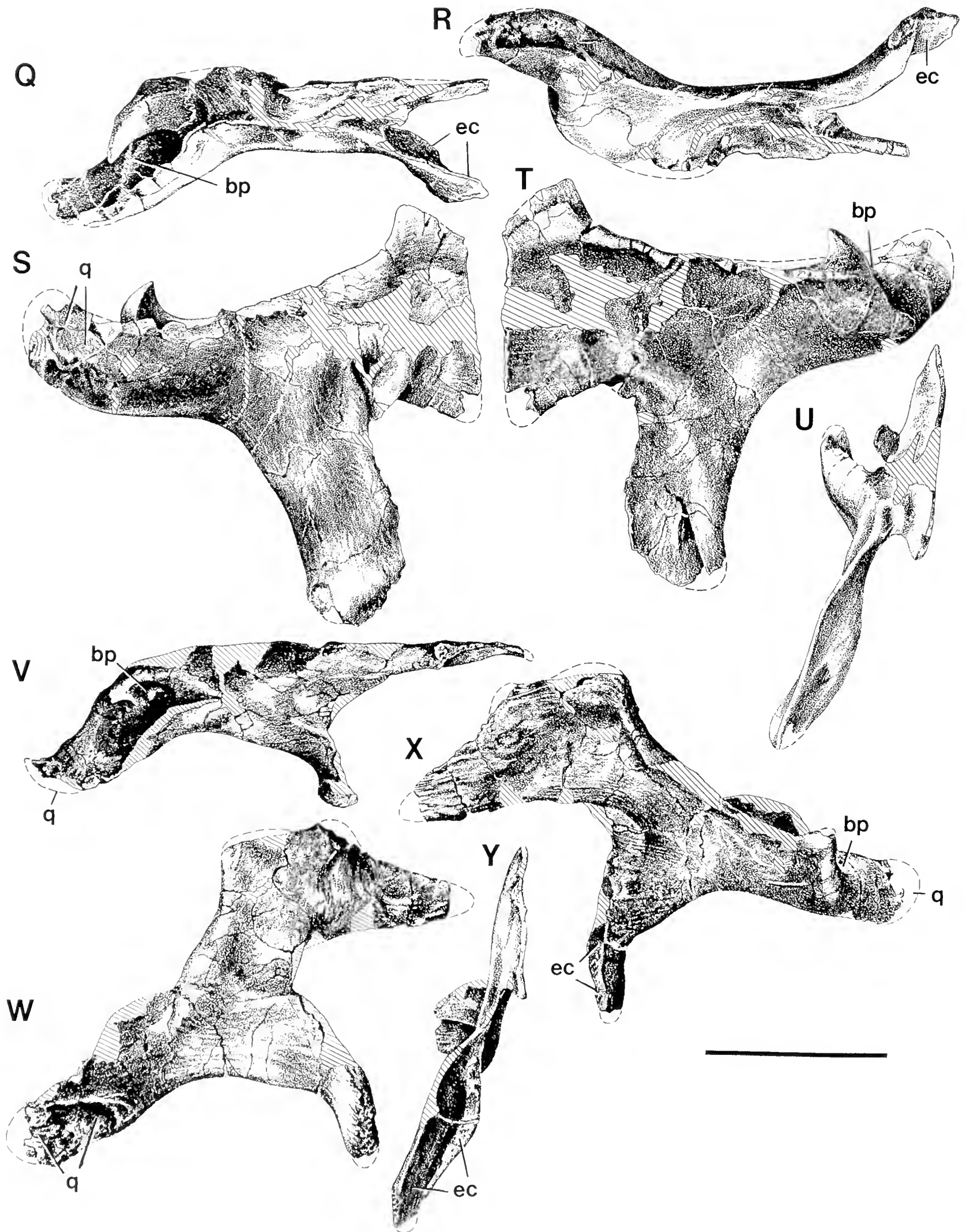


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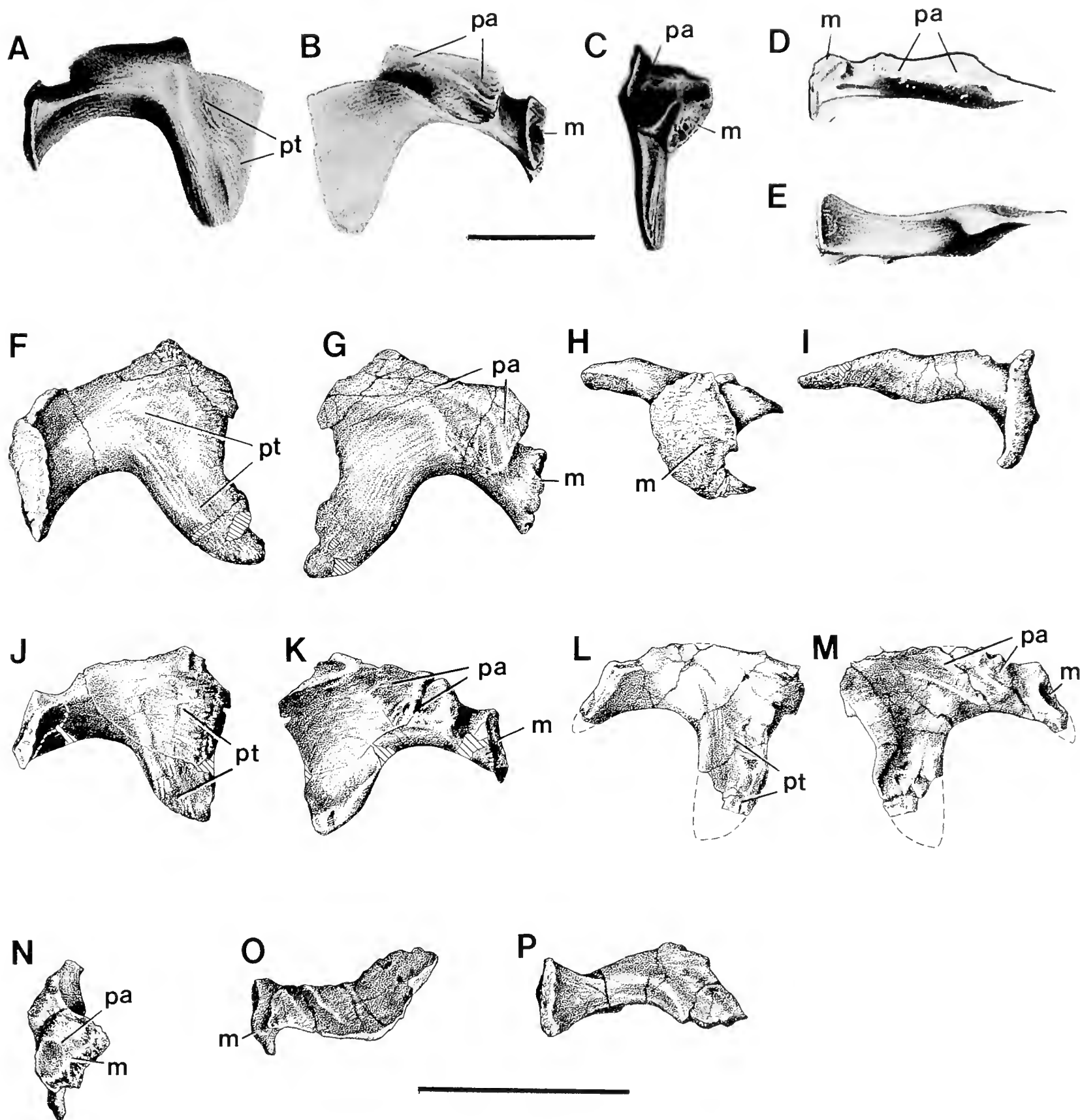


Fig. 37.—Ectopterygoids of *Camarasaurus*. A–E, *Camarasaurus grandis* YPM 1912 (l); F–I, *Camarasaurus* sp. UUVP 5115 (l); J, K, *Camarasaurus* sp. UUVP 4270 (l); L–P, *Camarasaurus lentus* DNM 28 (l). A, F, J, L, P, medial; B, G, K, M, N, lateral; D, H, O, dorsal; E, I, P, ventral; and C, N, anterior views. A–E, unpublished drawings prepared under the direction of Marsh. Scales, A–E = 5 cm; F–P = 10 cm.

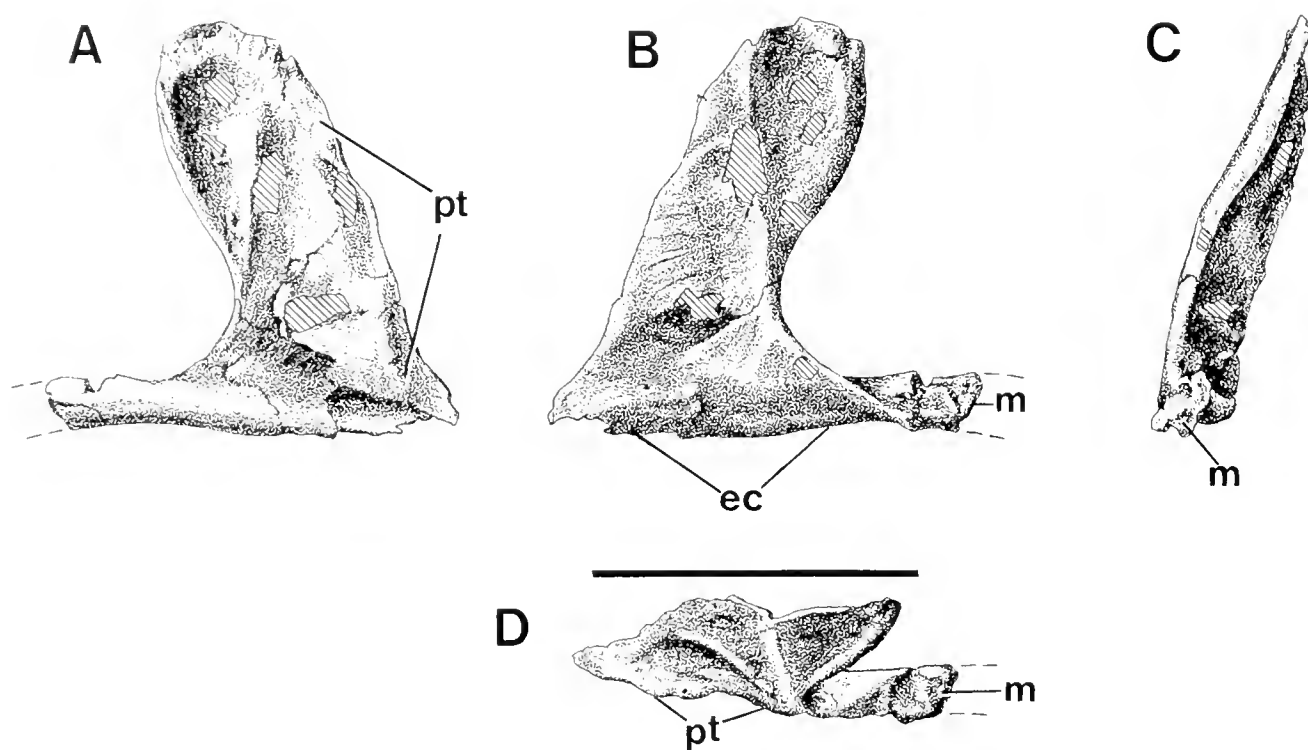


Fig. 38.—Right palatine of *Camarasaurus lentus* DNM 975. A, medial; B, lateral; C, anterior; and D, dorsal views. Scale = 10 cm.

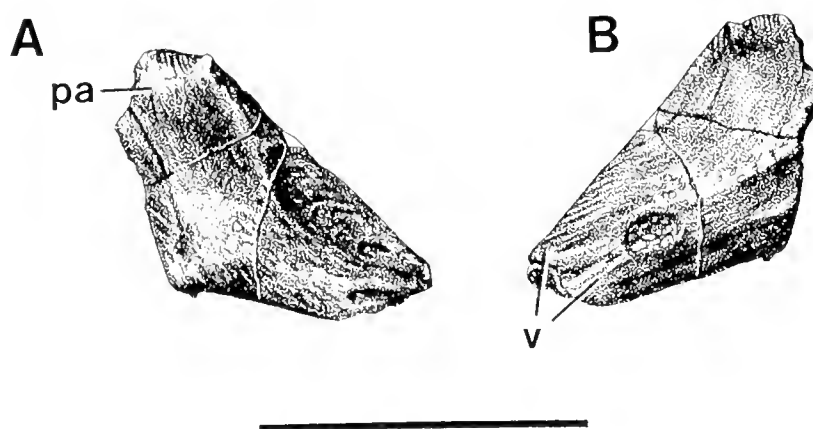


Fig. 39.—Right vomer of *Camarasaurus* sp. UUVP 5065. A, lateral; and B, medial views. Scale = 10 cm.

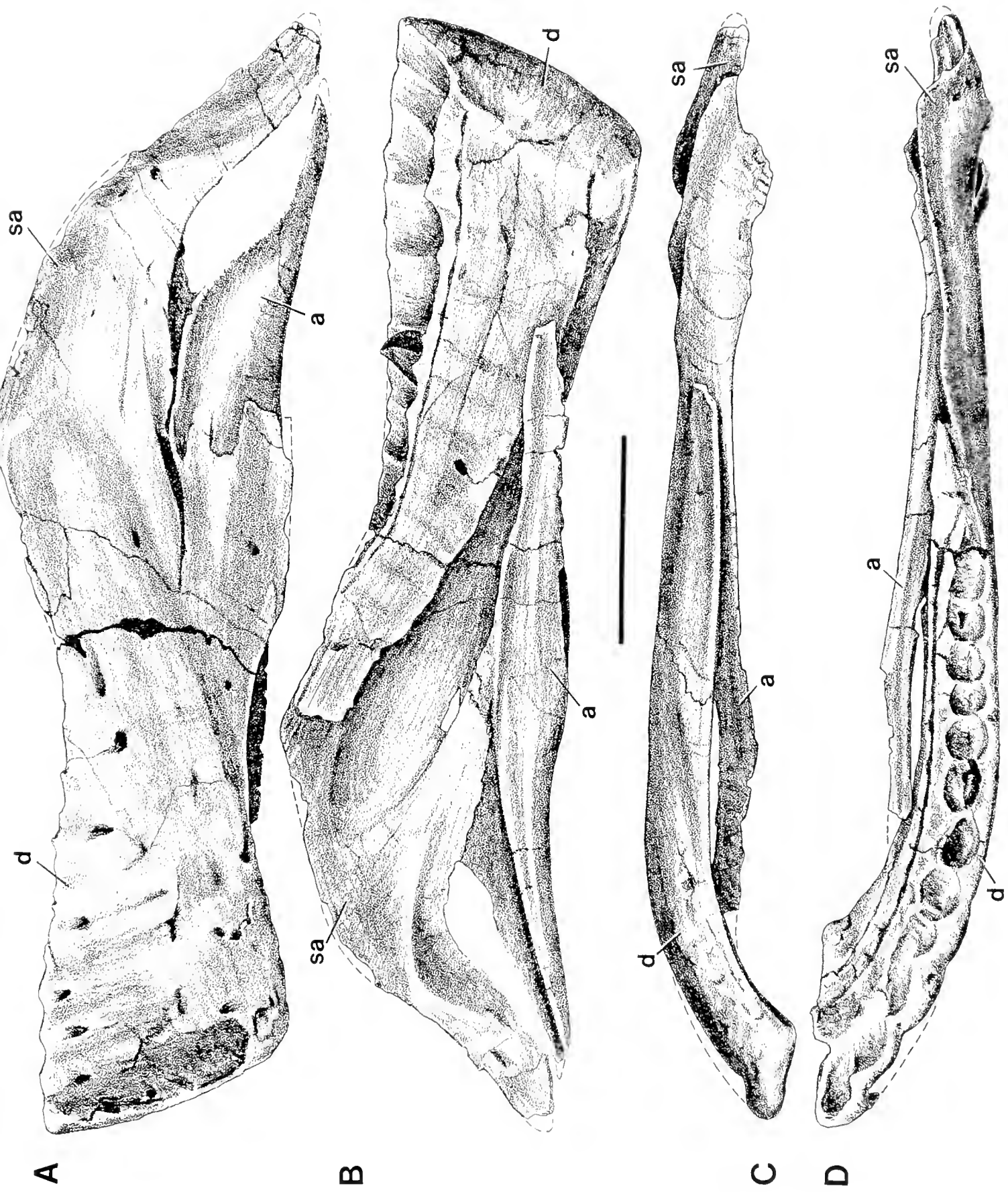


Fig. 40.—Partial left lower jaw of *Camarasaurus lentus* DNM 28. A, lateral; B, medial; C, ventral; and D, dorsal views. Scale = 10 cm.

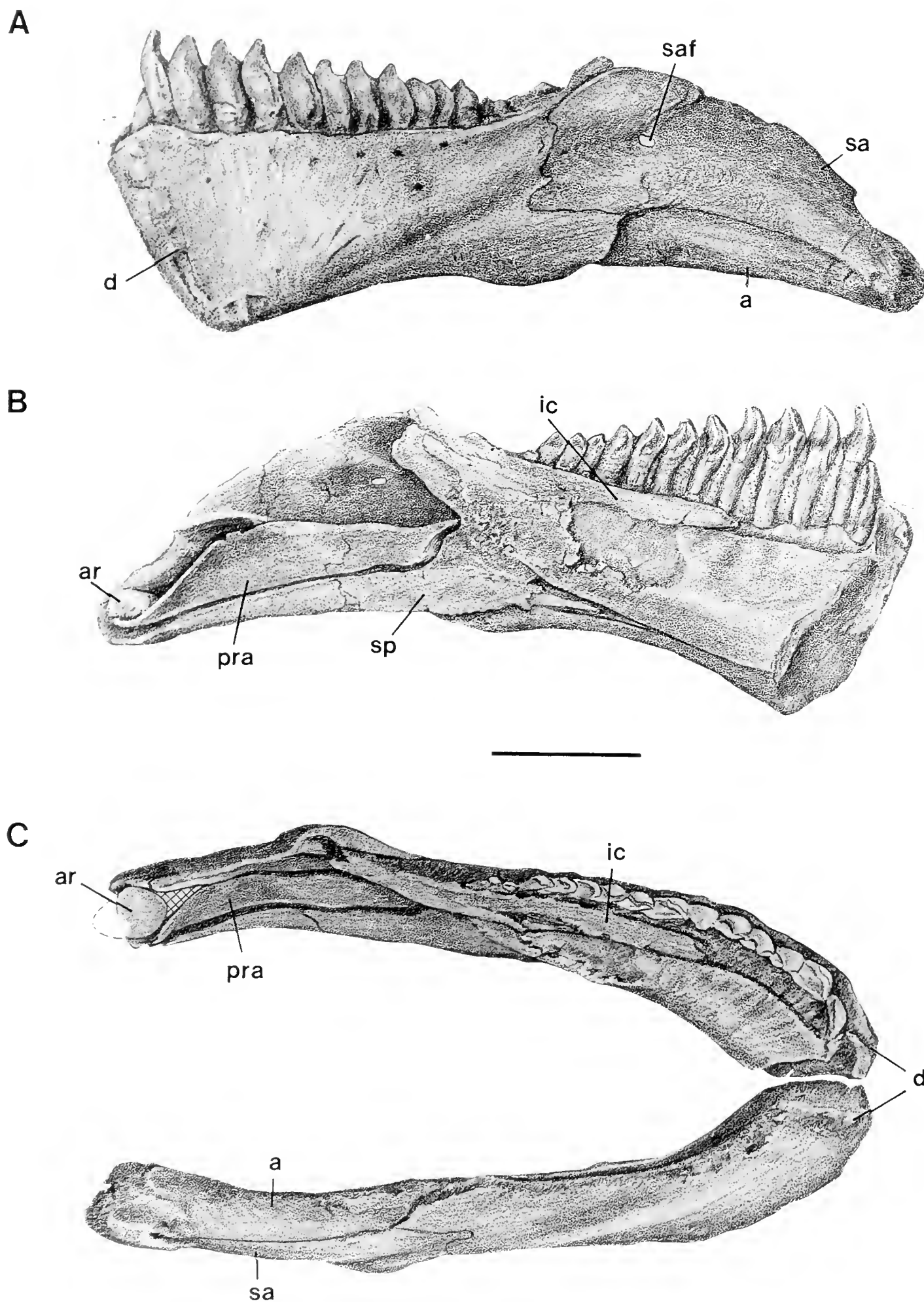


Fig. 41.—Left lower jaw of *Camarasaurus lentus* CM 11338. A, lateral; B, medial; C, ventral; and D, dorsal views. Scale = 10 cm.

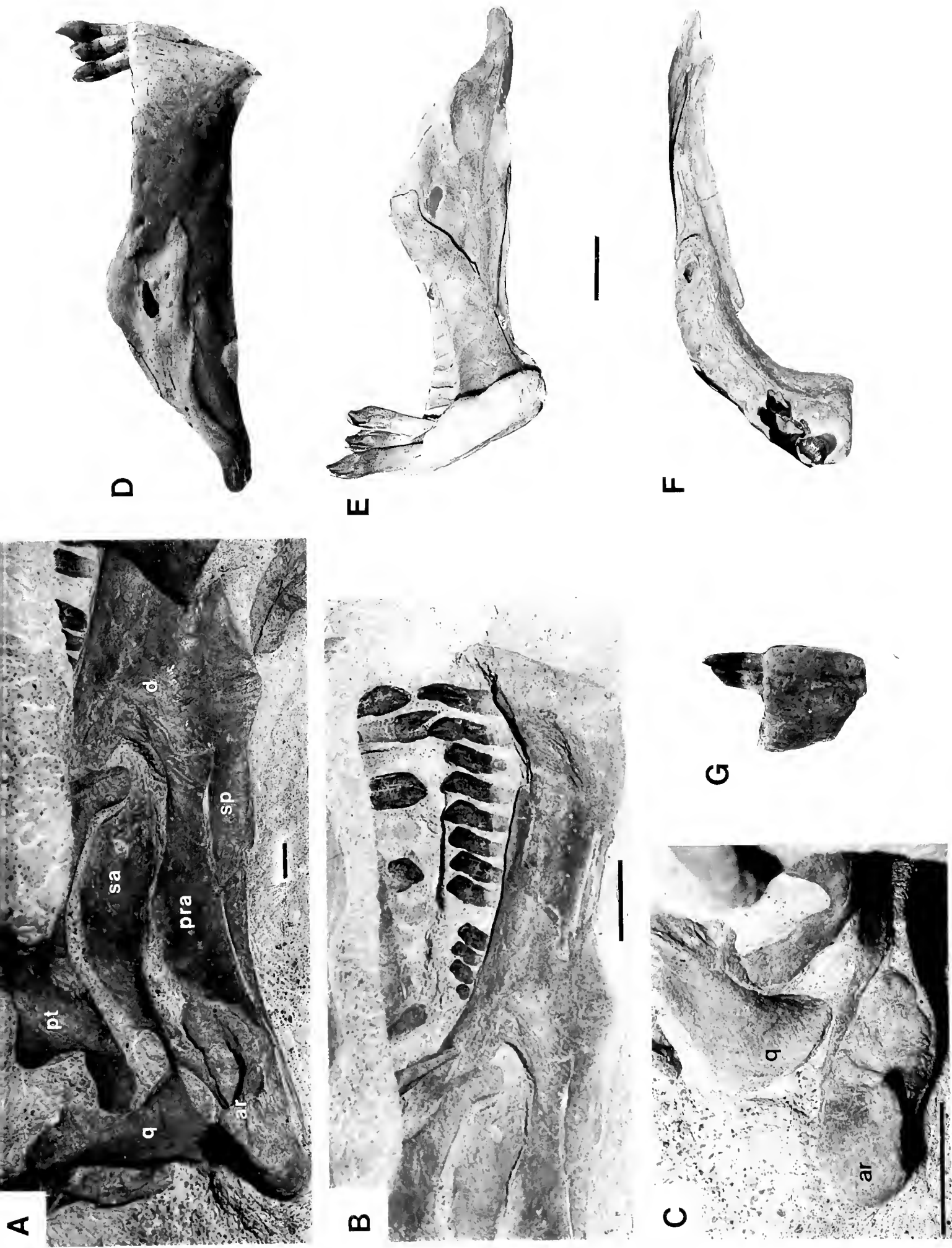


Fig. 42.—Lower jaw of *Camarasaurus lentus* DNM 975. A, medial view of posterior portion of left ramus (partly hidden by left pterygoid); B, medial view of anterior portion of left ramus; C, dorsal view of articular of left ramus. D, lateral; E, medial; F, dorsal; and G, anterior views of partial right ramus that includes the dentary, angular, and surangular. Scales = 5 cm.

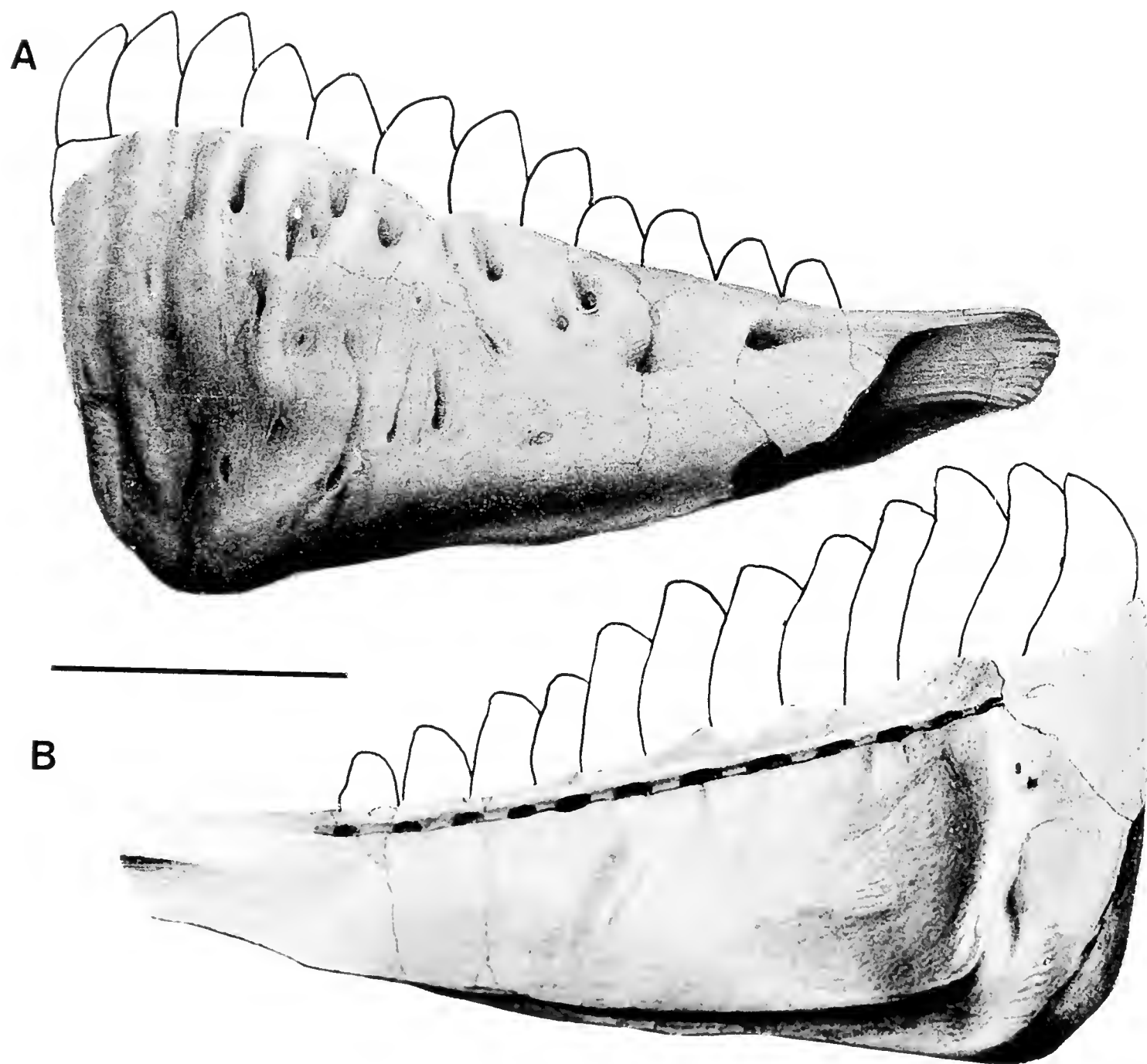


Fig. 43.—Left dentary of *Camarasaurus grandis*, paratype, YPM 1905. A, lateral; and B, medial views. A, taken from Marsh (1896); and B, prepared under direction of Marsh but not published. Scale = 5 cm.

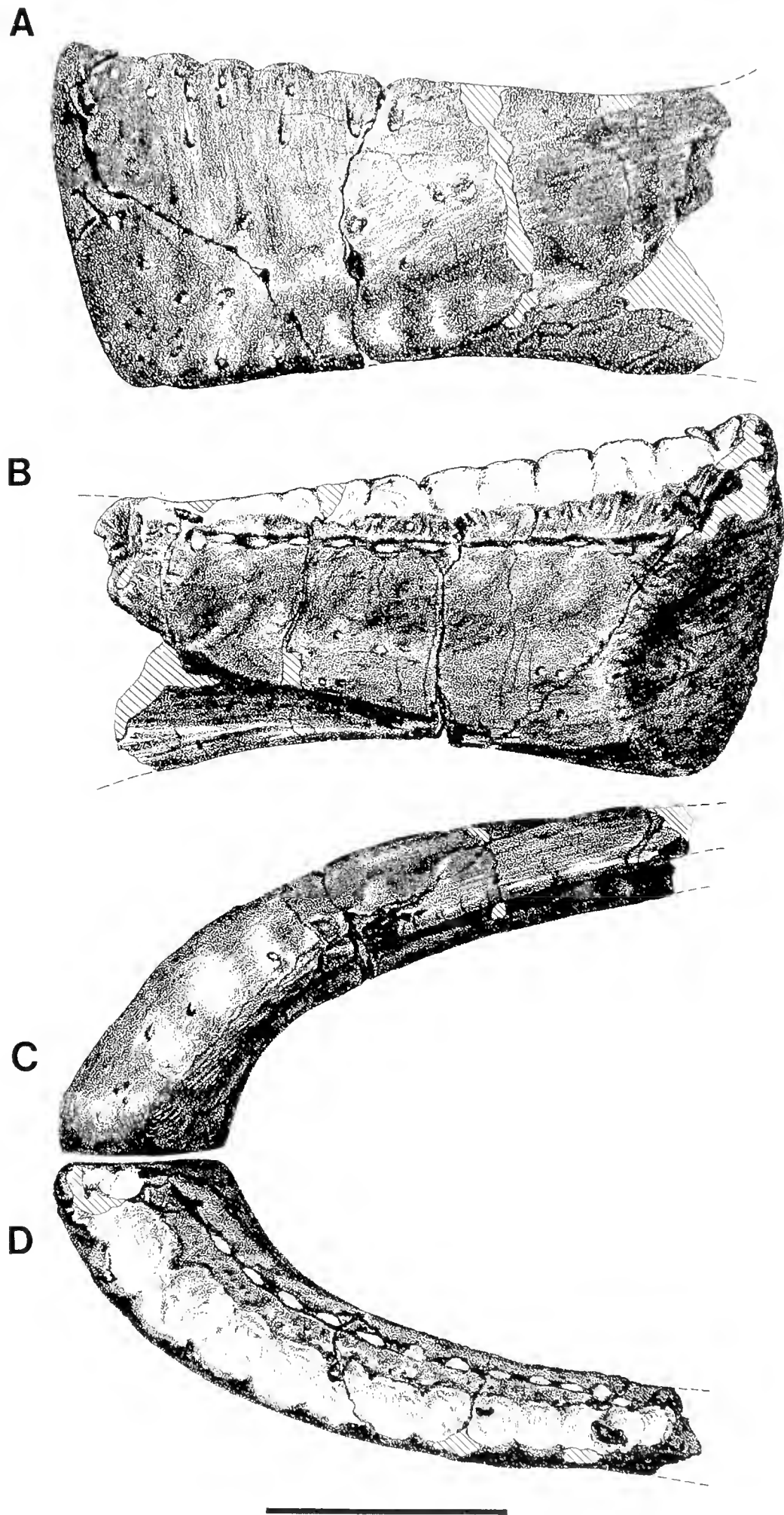


Fig. 44.—Left dentary of *Camarasaurus* sp. UUVP 3609. A, lateral; B, medial; C, ventral; and D, dorsal views. Scale = 10 cm.

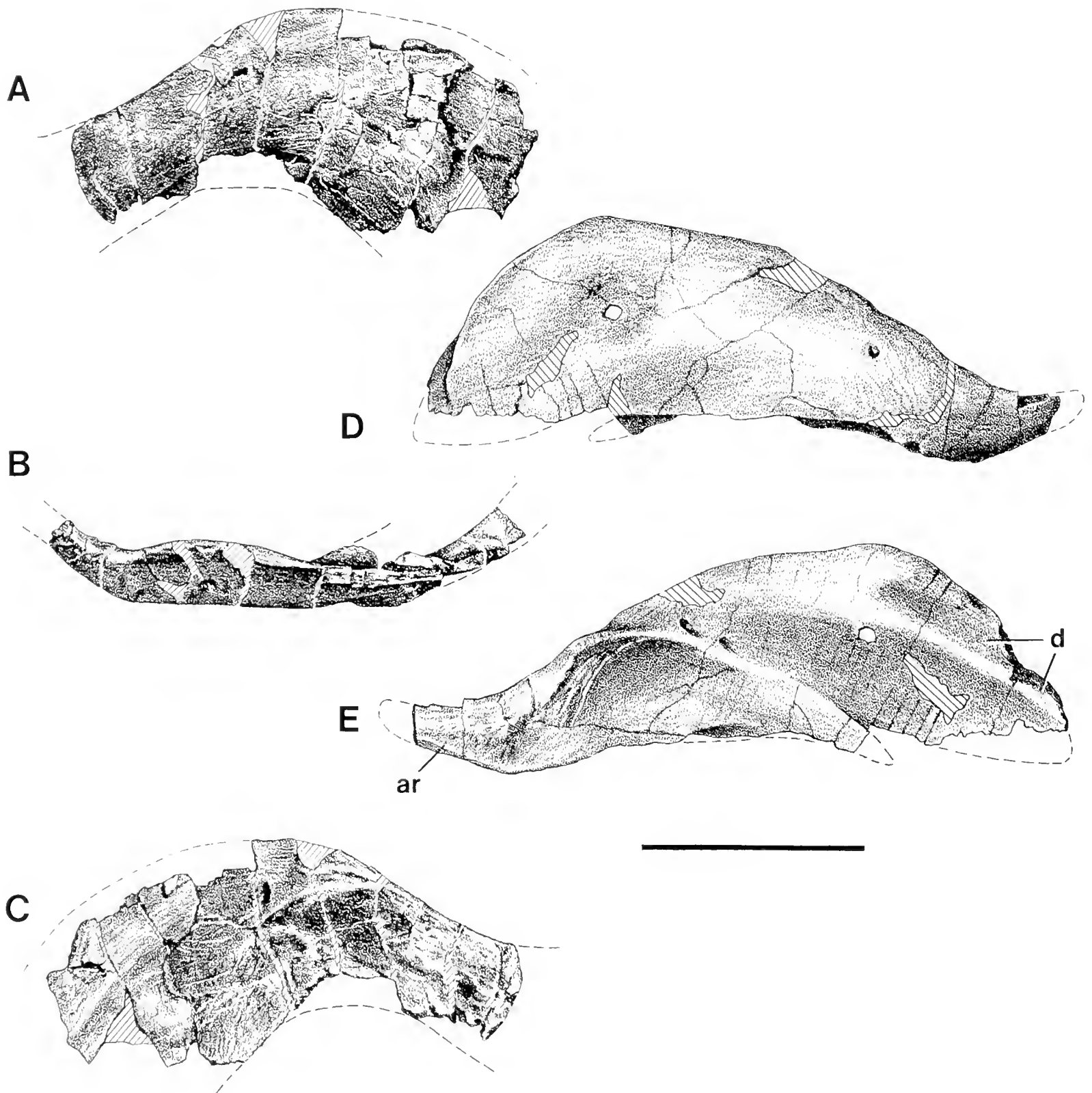


Fig. 45.—Surangulars of A–C, *Camarasaurus* sp. UUVP 6820 (r); D, E, *Camarasaurus* sp. UUVP 10065 (l); F–H, *Camarasaurus* sp. UUVP 3221 (r); and I–K, *Camarasaurus*-like skull *b* UUVP 10795 (r). A, D, F, I, lateral; B, G, J, dorsal; and C, E, H, K, medial views. Scales = 10 cm.

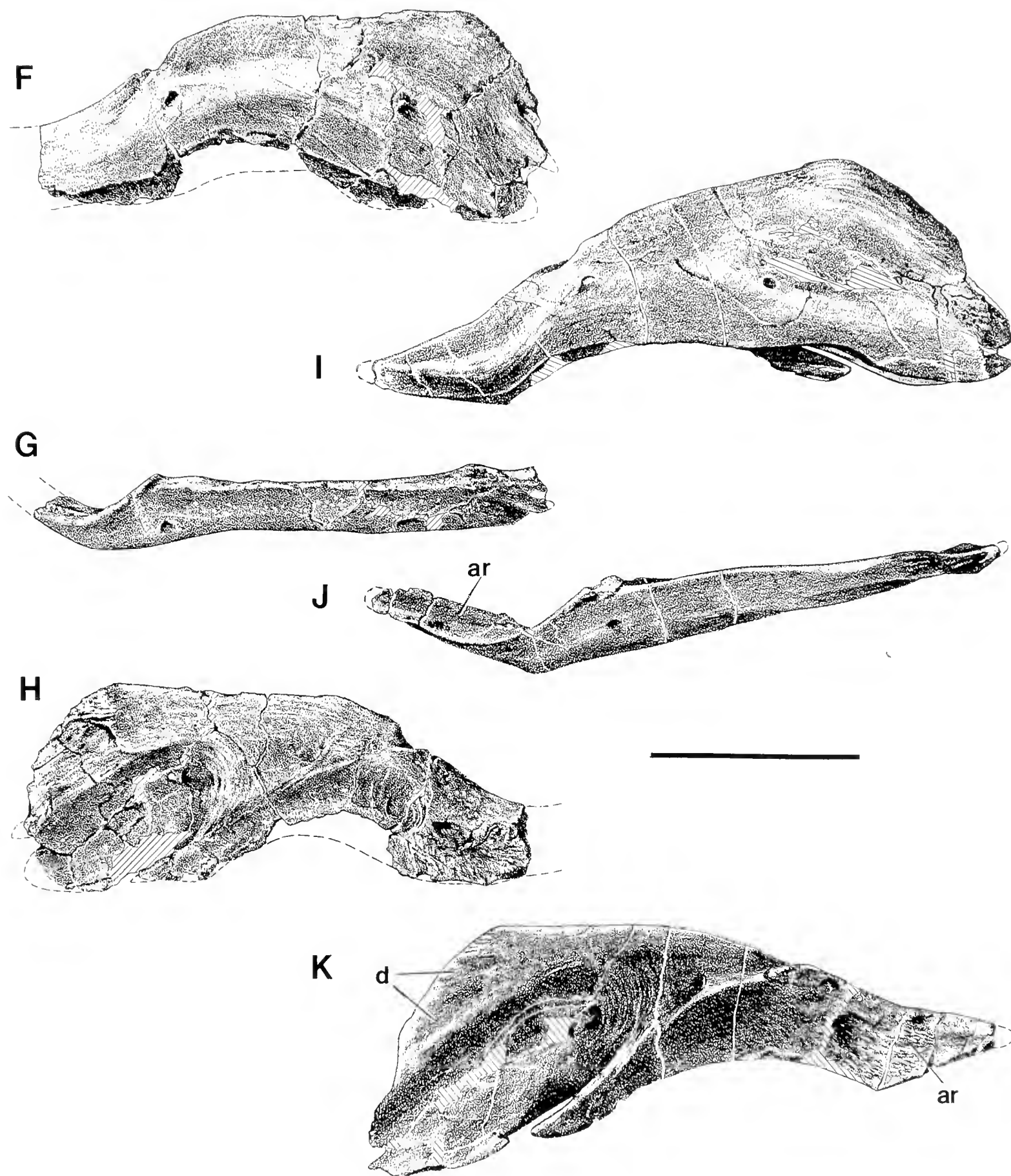


Fig. 45.—Continued.

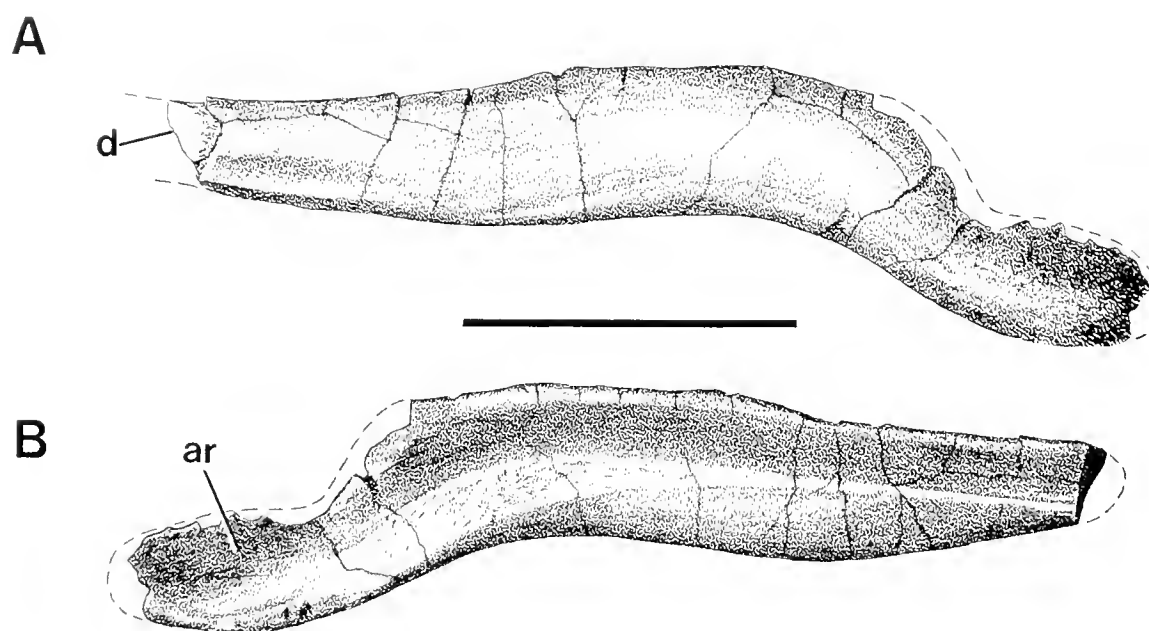


Fig. 46.—Left angular of *Camarasaurus* sp. UUV 10068. A, lateral; and B, medial views. Scale = 10 cm.

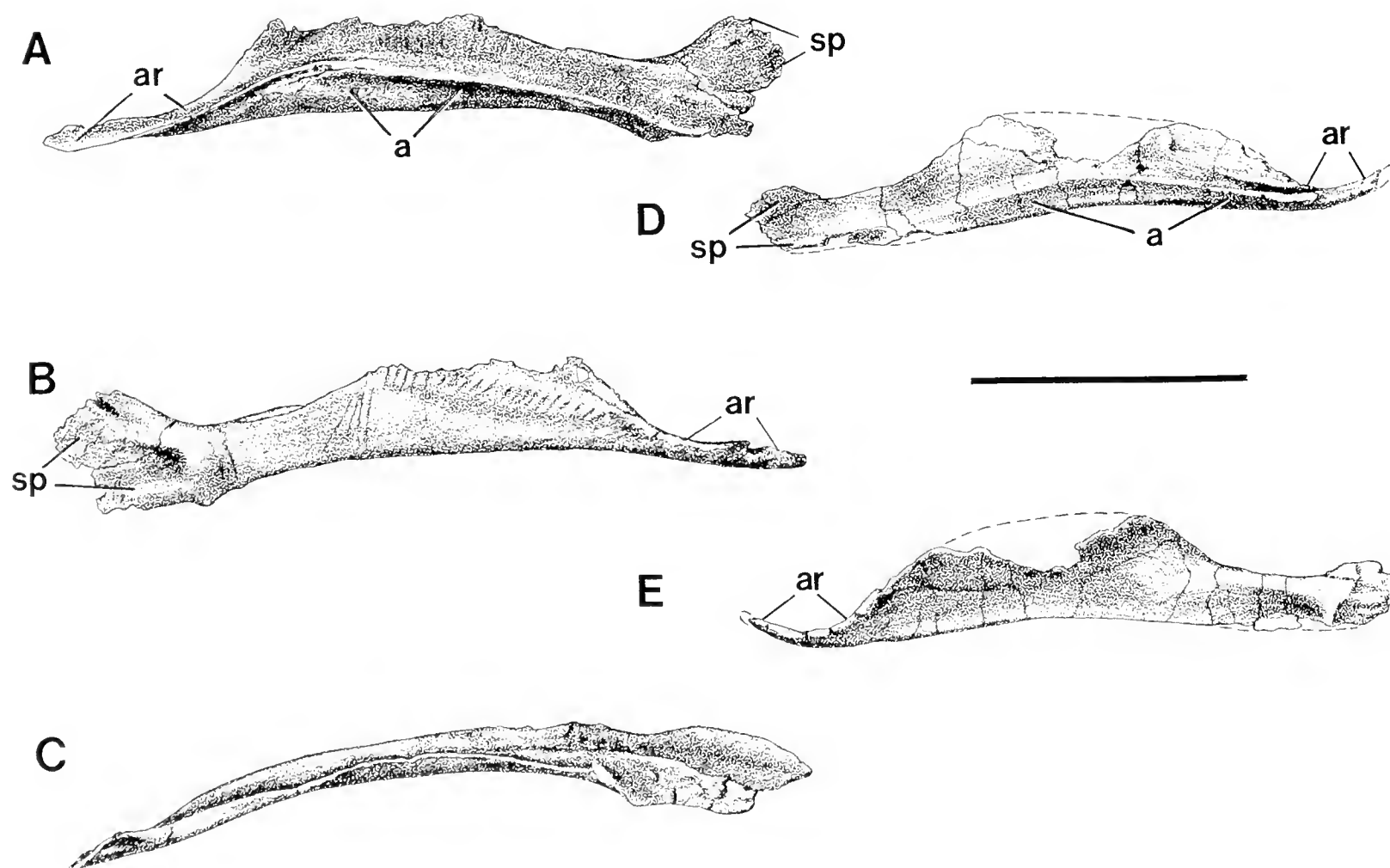


Fig. 47.—Preatriculars of *Camarasaurus lentus*. A–C, DNM 975 (r); and D, E, DNM 28 (l). A, D, medial; B, E, lateral; and C, dorsal views. Scale = 10 cm.

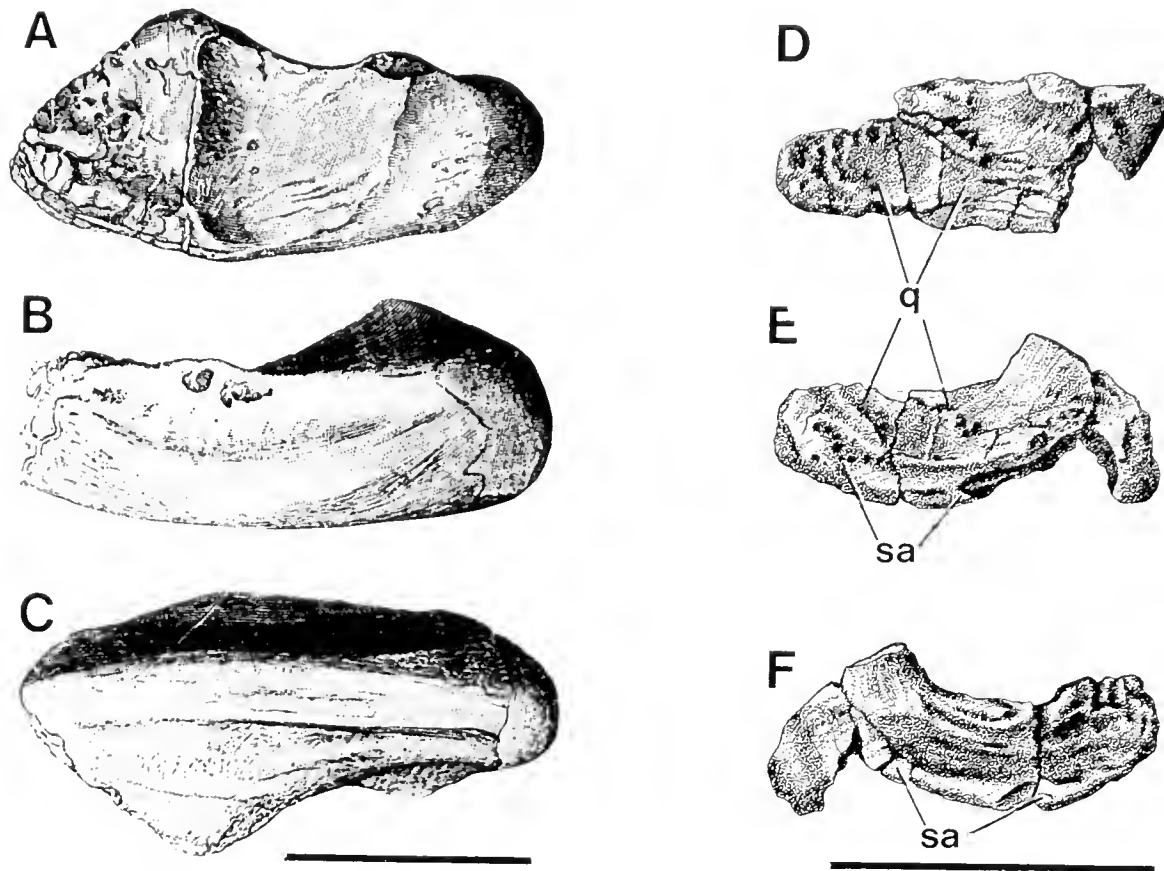


Fig. 48.—Articulars of *Camarasaurus*. A–C, *C. grandis*, YPM 1907 (l); and D–F, *Camarasaurus* sp. UUVP 4939 (l). A, D, dorsal; B, E, lateral; C, ventral; and F, medial views. A–C, unpublished drawings prepared under the direction of Marsh. Scales, A–C = 5 cm; D–F = 10 cm.

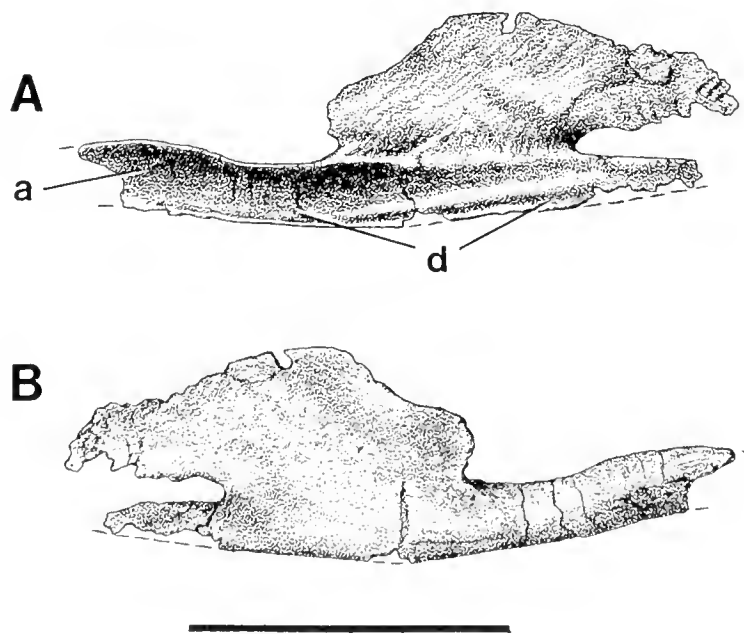


Fig. 49.—Right splenial of *Camarasaurus lentus* DNM 975. A, lateral; and B, medial views. Scale = 10 cm.

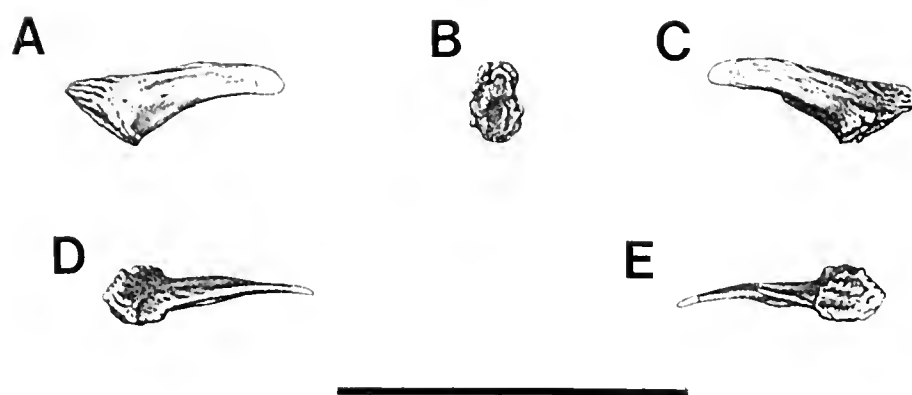


Fig. 50.—Left proatlas of *Camarasaurus grandis*, paratype, YPM 1905. A, lateral; B, anterior; C, medial; D, dorsal; and E, ventral views. Drawings prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966), who misidentified the proatlas as the postfrontal. Scale = 10 cm.

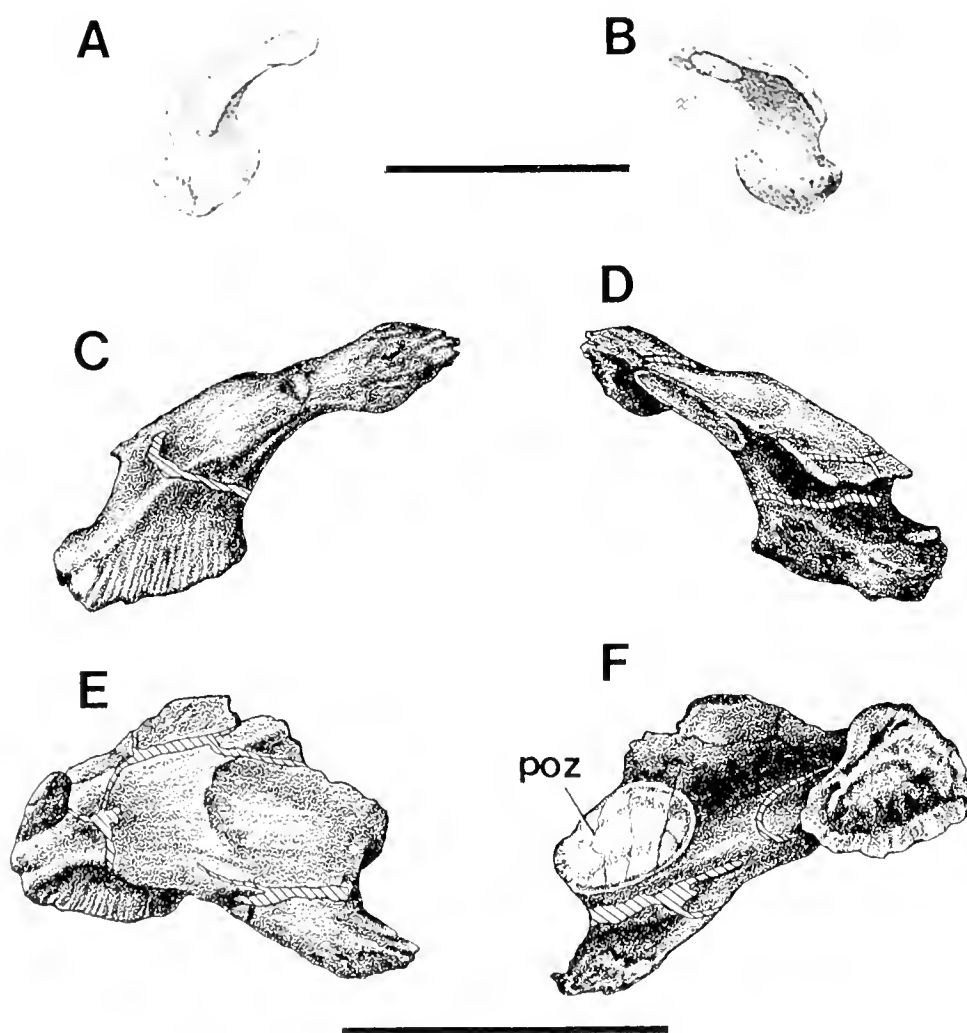


Fig. 51.—Left neurapophyses of the atlantes of *Camarasaurus*. A, B, C. *grandis*, paratype, YPM 1905; and C–F, *Camarasaurus* sp. UUVP 3467. A, C, lateral; B, D, medial; E, dorsal; and F, ventral views. A, B, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviation Z' indicating postzygapophysis. Scales = 10 cm.

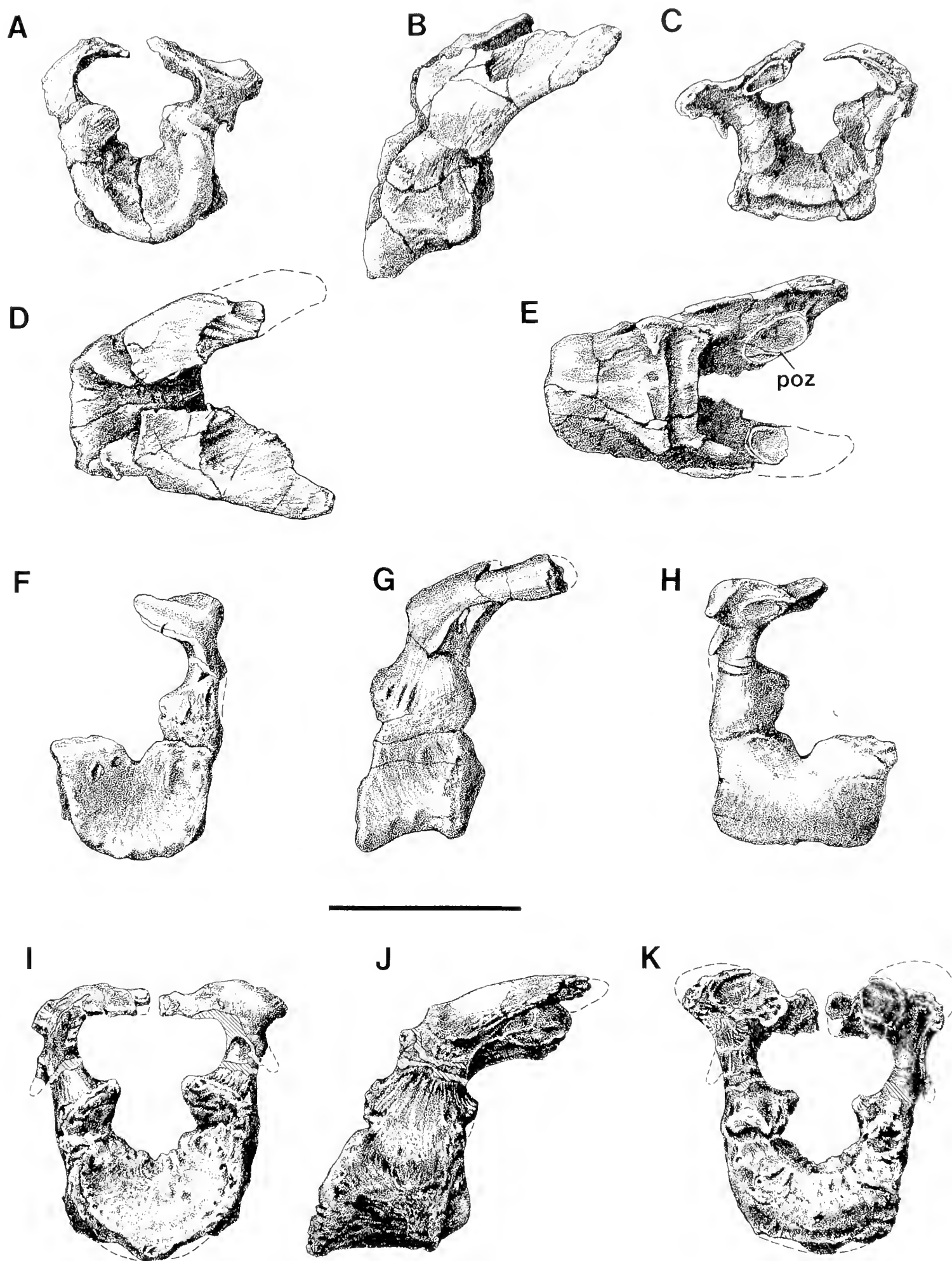


Fig. 52.—Atlantes of *Camarasaurus*. A–E, *C. lentus* DNM 28; F–H, *Camarasaurus* sp. UUV 10070; and I–K, *Camarasaurus* sp. UUV 2983. A, F, I, anterior; B, G, J, lateral; C, H, K, posterior; D, dorsal; and E, ventral views. Scale = 10 cm.

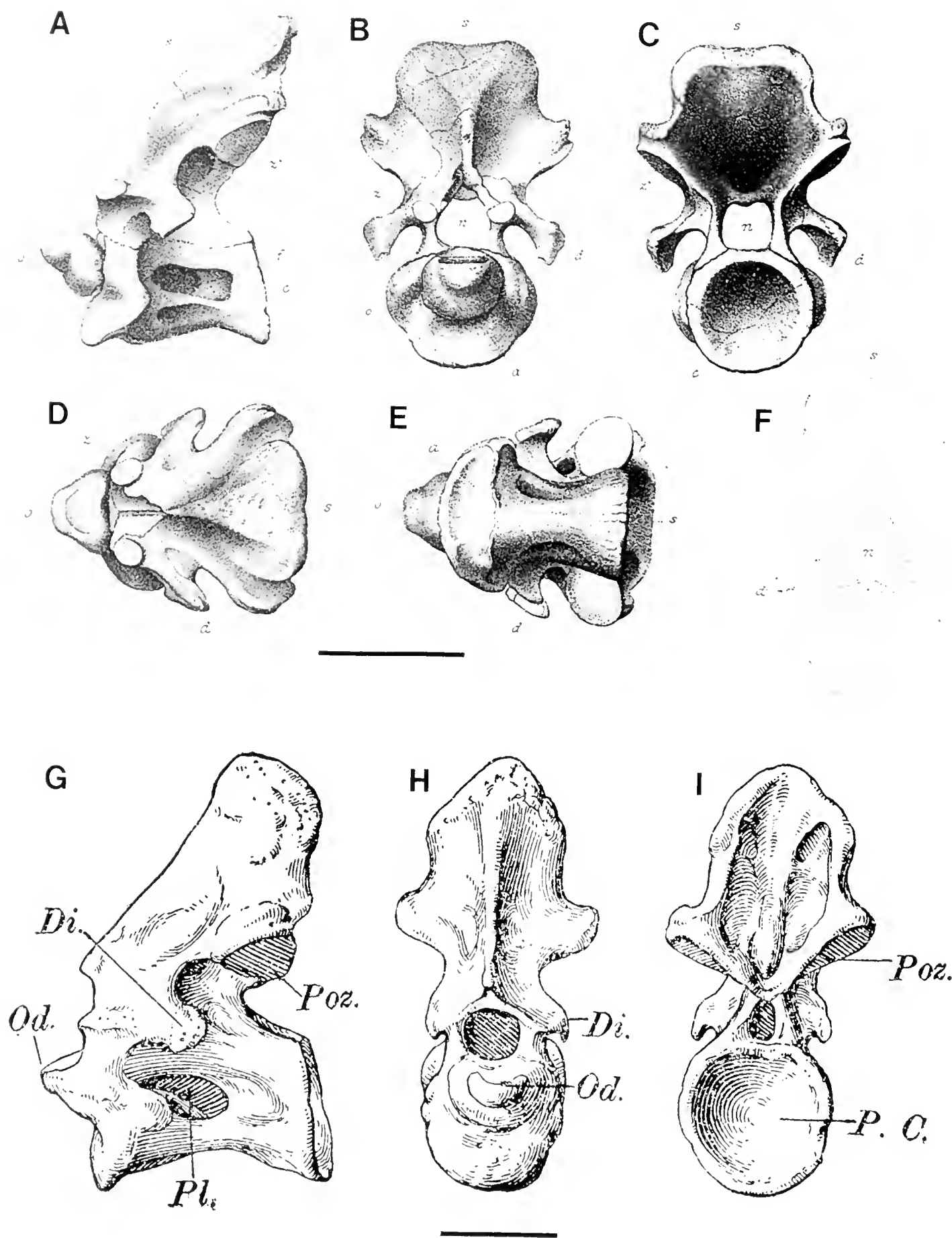


Fig. 53.—Axes of *Camarasaurus*. A–F, *C. grandis*, paratype, YPM 1905; G–I, *C. supremus* AMNH 5761; J–N, *C. lentus* DNM 288; O–S, *Camarasaurus* sp. UUVF 4273; T–X, *Camarasaurus* sp.; and Y–CC, *Camarasaurus* sp. UUVF 6341. A, G, J, O, T, Y, lateral; B, H, K, P, U, Z, anterior; C, I, L, Q, V, AA, posterior; D, M, R, W, BB, dorsal; and E, N, S, X, CC, ventral views. F, transverse section of axis. A–F, prepared under the direction of Marsh but published for the first time by Ostrom and McIntosh (1966) with abbreviations as follows: a, intercentrum of the axis; c, centrum; d, diapophysis; f, lateral pleurocoel; n, neural canal; o, odontoid process; s, neural spine; z, prezygapophysis; z', postzygapophysis. G–I after Osborn and Mook (1921) and abbreviations as in that paper: Di., diapophysis; Od., odontoid; P.C., posterior end of centrum; Pl., pleurocoel; Poz., posterior zygapophysis. Scales = 10 cm.

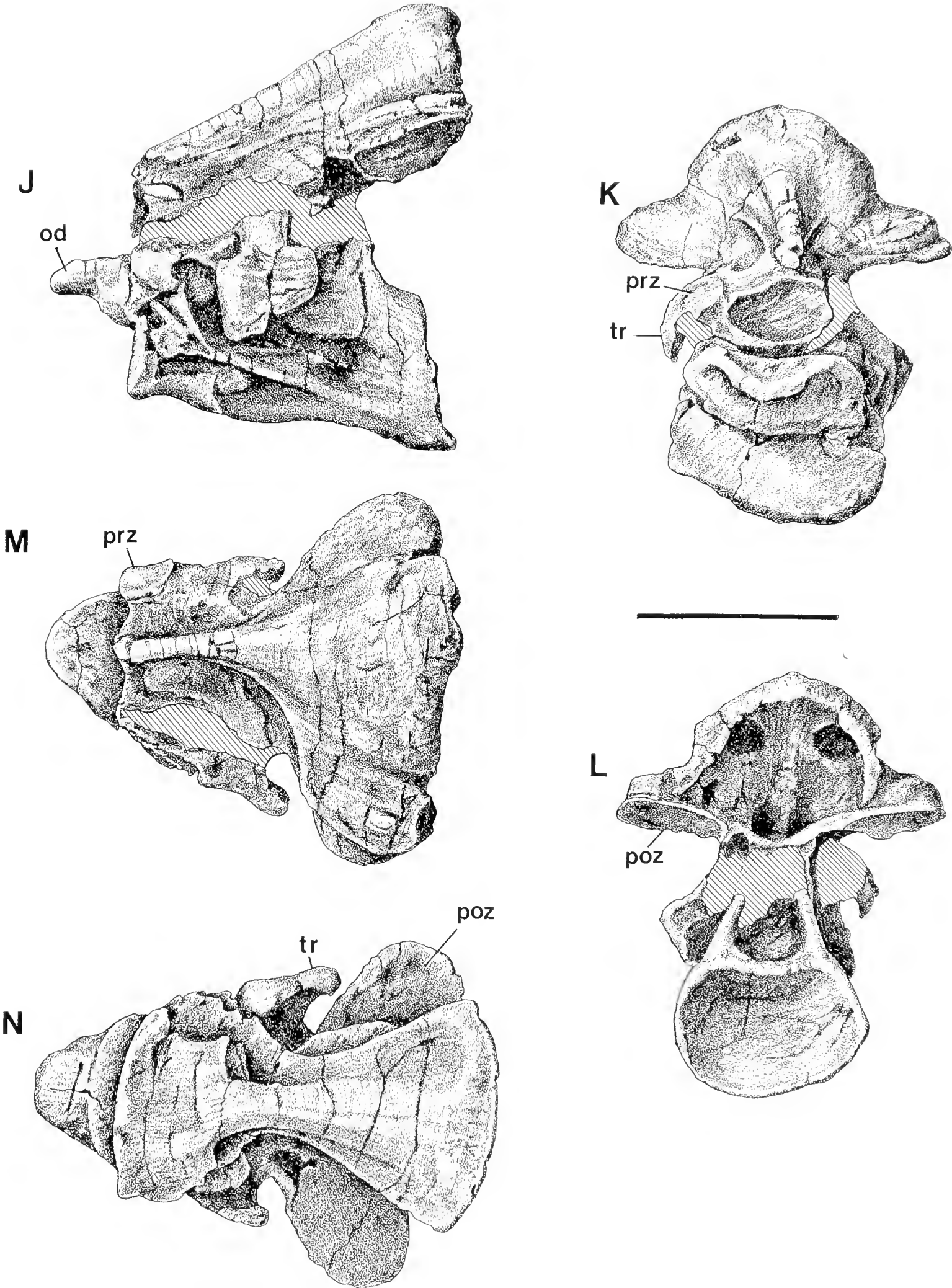


Fig. 53.—Continued.

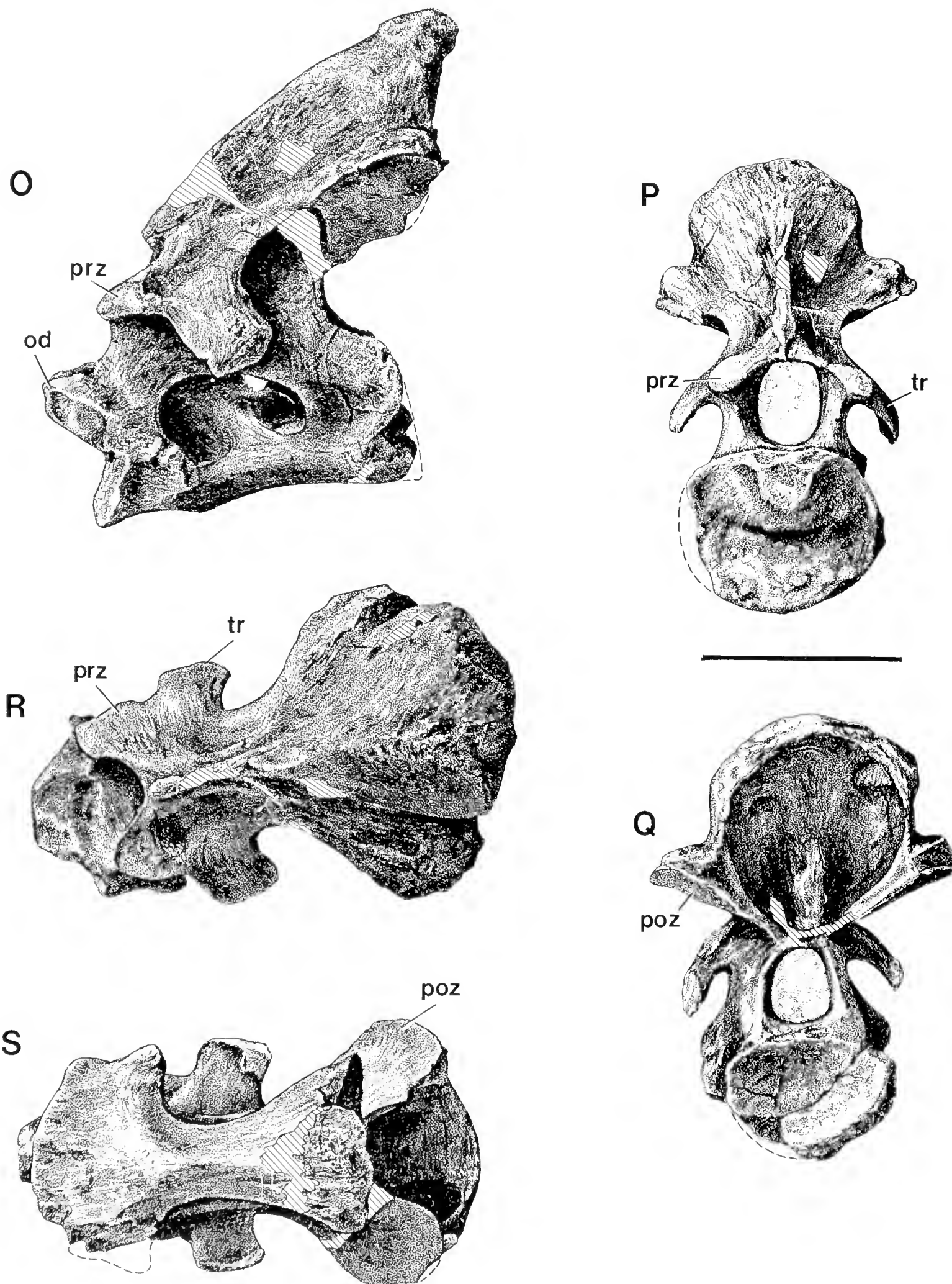


Fig. 53.—Continued.

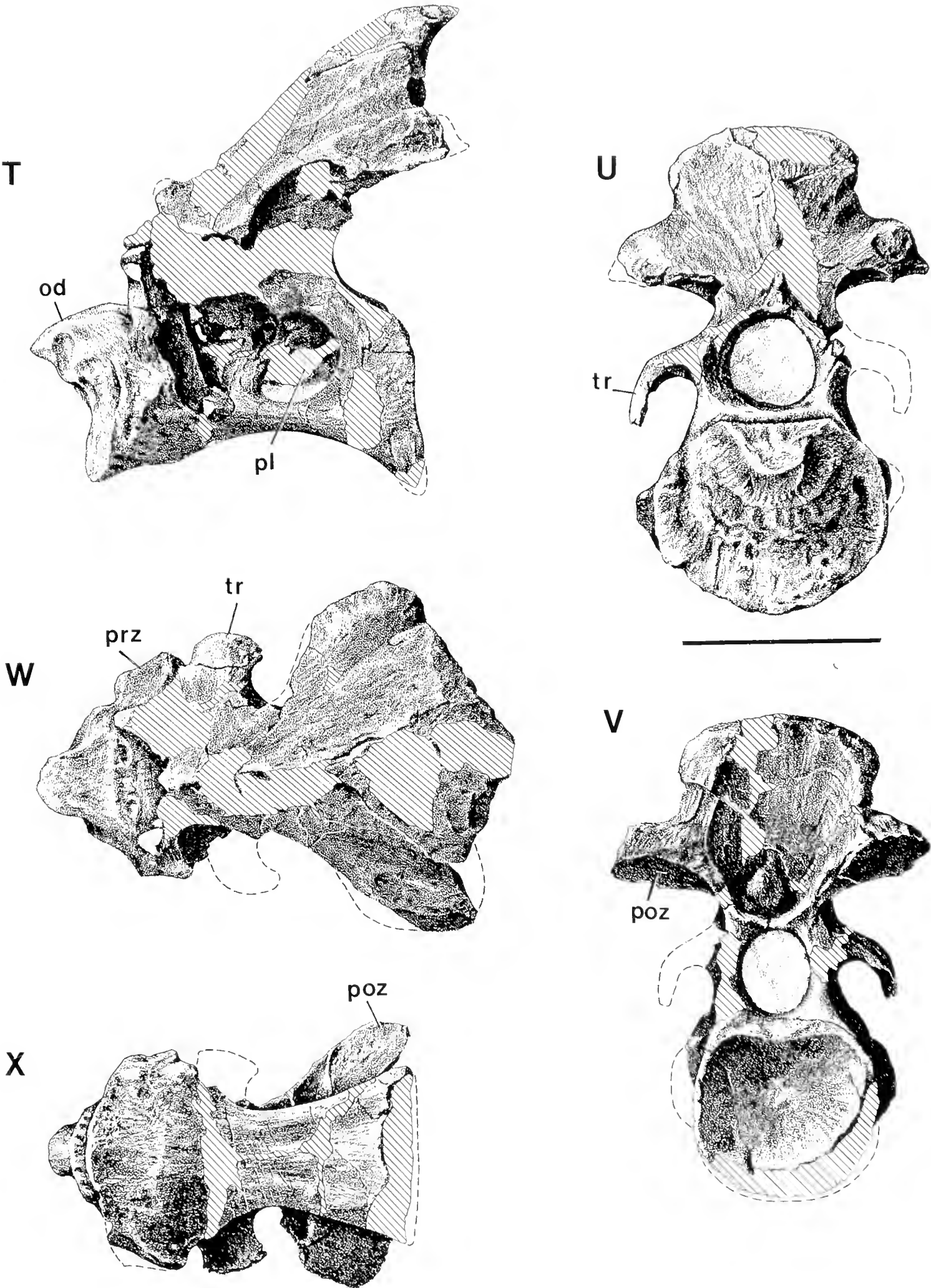


Fig. 53.—Continued.

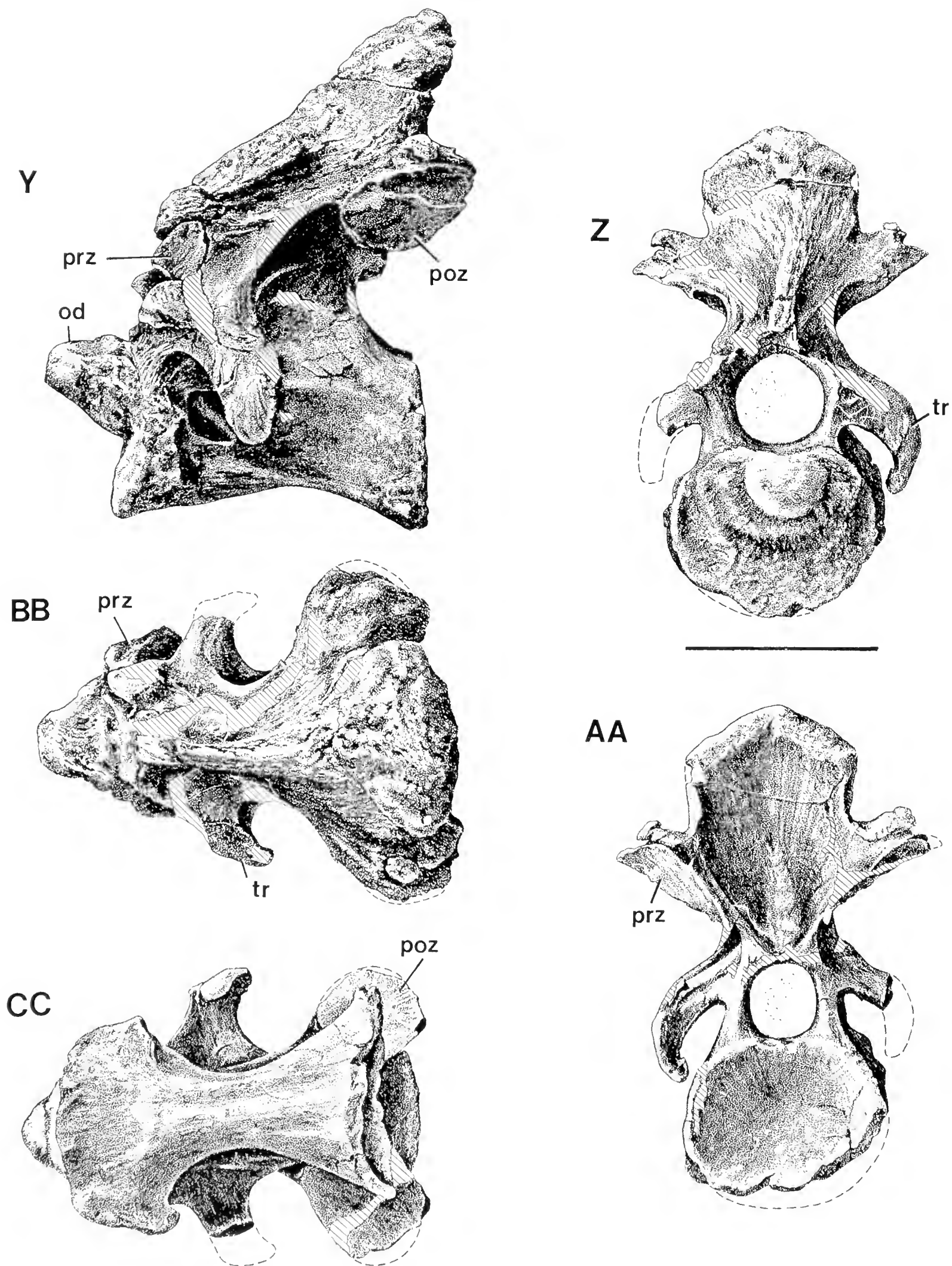


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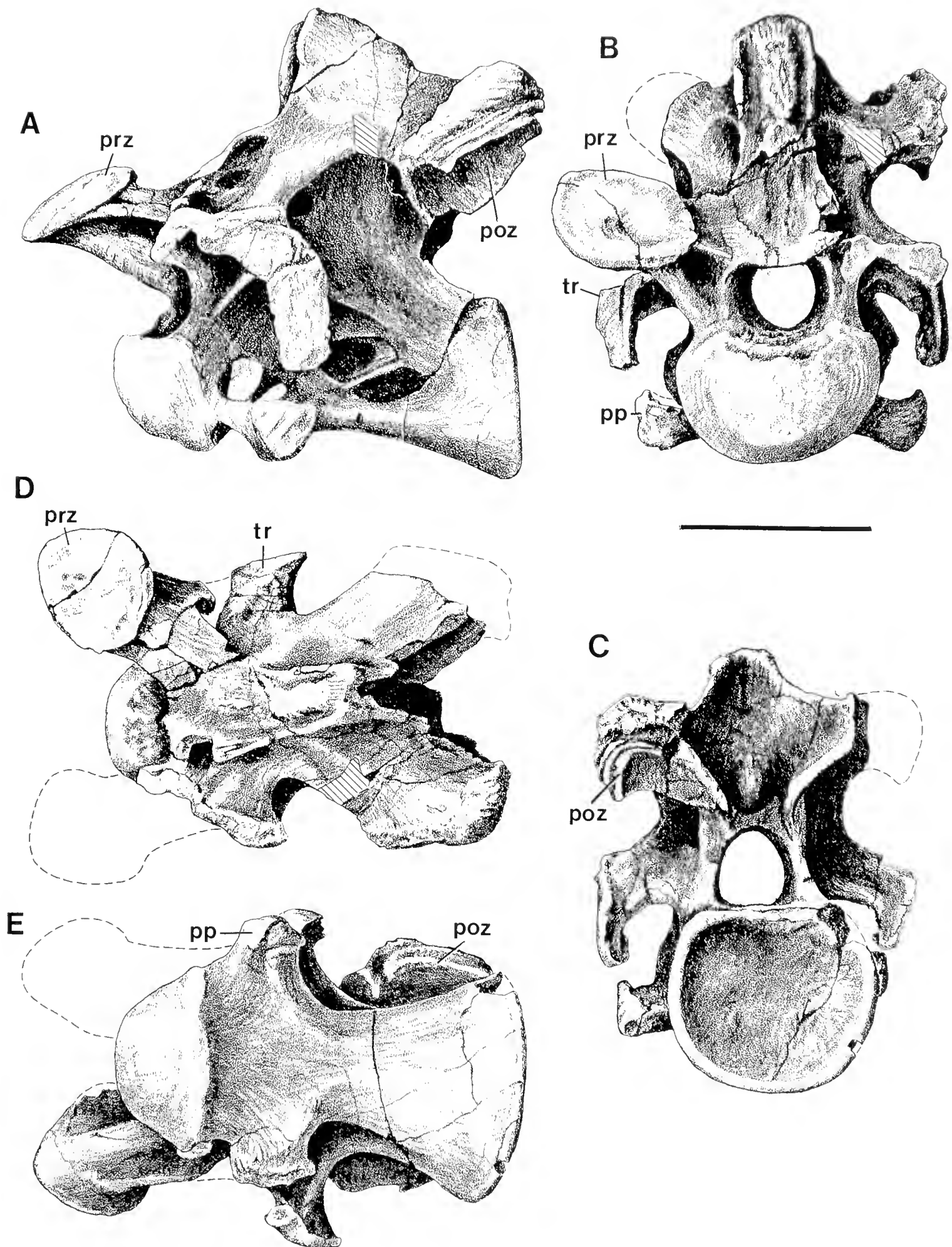


Fig. 54.—Cervical 3 of *Camarasaurus* sp. UUVP 10896. A, lateral; B, anterior; C, posterior; D, dorsal; and E, ventral views. Scale = 10 cm.

BULLETIN

OF CARNEGIE MUSEUM OF NATURAL HISTORY



PHYLOGENETIC SYSTEMATICS OF
CROTAPHYTID LIZARDS
(REPTILIA: IGUANIA: CROTAPHYTIDAE)

JIMMY A. McGUIRE

